

1909

Pushnik, J.C., R.S. Demaree, J.L.J. Houps, W.B. Flory, S.M. Bauer, and P.D. Anderson. 1995. The effect of elevated carbon dioxide on a Sierra-Nevadan dominant species: *Pinus ponderosa*. *Journal of Biogeography* 22(2-3):249-254.

The impact of increasing atmospheric CO₂ has not been fully evaluated on western coniferous forest species. Two year old seedlings of *Pinus ponderosa* were grown in environmentally controlled chambers under increased CO₂ conditions (525 μ mol L⁻¹ and 700 μ mol L⁻¹) for 6 months. These trees exhibited morphological, physiological and biochemical alterations when compared to our controls (350 μ mol L⁻¹). Analysis of whole plant biomass distribution has shown no significant treatment effect to the root to shoot ratios. However, while stem diameter and height growth generally increased with elevated CO₂, needles exhibited an increased overall specific needle mass and a decreased total needle area. Morphological changes at the needle level included decreased mesophyll to vascular tissue ratio and variations in starch storage in chloroplasts. The elevated CO₂ increased internal CO₂ concentrations and assimilation of carbon. Biochemical assays revealed that ribulose-bis-phosphate carboxylase (RuBPCase) specific activities increased on per unit area basis with CO₂ treatment levels. Sucrose phosphate synthase (SPS) activities exhibited an increase of 55% in the 700 μ mol L⁻¹ treatment. These results indicate that the sink-source relationships of these trees have shifted carbon allocation toward above ground growth, possibly due to transport limitations.

KEYWORDS: ATMOSPHERIC CO₂, CO₂- ENRICHMENT, FORMS, GROWTH, LEAF ANATOMY, PHOTOSYNTHETIC ACCLIMATION, RADIATA, SEEDLINGS, SUCROSE PHOSPHATE SYNTHASE, TREES

1910

Pushnik, J.C., D. Garcia-Ibancieta, S. Bauer, P.D. Anderson, J. Bell, and J.L.J. Houps. 1999. Biochemical responses and altered genetic expression patterns in ponderosa pine (*Pinus ponderosa* Doug ex P. Laws) grown under elevated CO₂. *Water, Air, and Soil Pollution* 116(1-2):413-422.

Biochemical and gene expression changes in response to elevated atmospheric CO₂ were investigated in five maternal half-sibling breeding families of Ponderosa pine. Seedlings were grown in a common garden located at Lawrence Livermore National Laboratory, in open-topped chambers (OTC) for two years. Chamber atmospheres were maintained at ambient, ambient + 175 μ mol L⁻¹ CO₂, or ambient + 350 μ mol L⁻¹ CO₂. Growth measurements showed significant increases in stem volumes and volume enhancement ratios in three of the five families studied when grown under elevated CO₂. Biochemical and gene expression studies were undertaken to gain a mechanistic understanding of these phenotypic responses. Biochemical studies focused on sucrose phosphate synthase (SPS) specific activities at increase CO₂ levels. Kinetic evaluations of SPS showed an increase in V-Max. Specific SPS probes revealed increases in the transcriptional levels of one SPS gene with exposure to increasing CO₂. RT-PCR differential gene displays showed that overall only a small fraction of visualized gene transcripts responded to elevated CO₂ (8-10%). There were also significant differences between the gene expression patterns of the different families, some of which correlated with alterations in growth at elevated CO₂ levels.

KEYWORDS: ALLOCATION, ANATOMY, CARBON-DIOXIDE ENRICHMENT, ENZYMES, LEAVES, METABOLISM, PROTEIN-PHOSPHORYLATION, SEEDLINGS, SUCROSE PHOSPHATE SYNTHASE, TREES

1911

Qi, J.E., J.D. Marshall, and K.G. Mattson. 1994. High soil carbon-dioxide concentrations inhibit root respiration of douglas-fir. *New Phytologist* 128(3):435-442.

Total and basal respiration (R(t) and R(b), respectively) of intact and undisturbed roots of one-year-old Douglas fir seedlings, *Pseudotsuga menziesii* var. *glauca* [Beissn] France, were measured at experimentally varied soil carbon dioxide concentrations ([CO₂]). Use of specially designed root boxes and a CO₂ gas-flow compensating system designed around an infrared gas analyzer (IRGA) allowed controlled delivery of CO₂ to roots and simultaneous measurements of CO₂ released by roots. Root respiration rate responded to each inlet [CO₂], independent of whether the previous concentration had been higher or lower, within two to three hours (paired t test = 0.041, P = 0.622, and n = 13). Total and basal respiration rates decreased exponentially as soil [CO₂] rose from 130 ppm, well below atmospheric [CO₂], to 7015 ppm, a concentration not uncommon in field soils. Analyses of variance (ANOVA) showed that the effects of soil [CO₂] on rates of total and basal root respiration were statistically significant. Root respiration rates decreased by 4 to 5 nmol CO₂ g⁻¹ dry weight of roots s⁻¹ for every doubling of [CO₂] according to the following equations: $\ln(R(t))$ (nmol CO₂ g⁻¹ s⁻¹) = $5.24 - 0.30 \cdot \ln[CO_2]$ with $r = 0.78$, $P < 0.0001$, and $n = 70$; and $\ln(R(b))$ (nmol CO₂ g⁻¹ s⁻¹) = $6.29 - 0.52 \cdot \ln[CO_2]$ with $r = 0.82$, $P < 0.0001$, and $n = 35$. The sensitivity of root respiration to [CO₂] suggests that some previous laboratory measurements of root respiration at atmospheric [CO₂], which is 3 to 10-fold lower than [CO₂] in field soils, overestimated root respiration in the field. Further, the potential importance of soil [CO₂] indicates that it should be accounted for in models of below-ground carbon budgets.

KEYWORDS: CO₂- ENRICHMENT, DARK RESPIRATION, EFFLUX, FIELD, GROWTH, LEAVES, LOLIUM-PERENNE, MAINTENANCE RESPIRATION, PERENNIAL RYEGRASS, SEEDLINGS

1912

Rabbinge, R., H.C. Vanlatesteijn, and J. Goudriaan. 1993. Assessing the greenhouse-effect in agriculture. *Ciba Foundation Symposia* 175:62-79.

Evidence that concentrations of CO₂ and trace gases in the atmosphere have increased is irrefutable. Whether or not these increased concentrations will lead to climate changes is still open to debate. Direct effects of increased CO₂ concentrations on physiological processes and individual plants have been demonstrated and the consequences for crop growth and production under various circumstances are evaluated with simulation models. The consequences of CO₂ enrichment are considerable under optimal growing conditions. However, the majority of crops are grown under sub-optimal conditions where the effects of changes in CO₂ are often less. The same holds for the possible indirect effects of environmental changes such as temperature rise. Studies on individual plants under optimal conditions are therefore not sufficient for evaluating the effects at a farm, regional, national or supra-national level. Simulation studies help to bridge the gap between the various aggregation levels and provide a basis for various studies of policy options at various aggregation levels.

KEYWORDS: CARBON DIOXIDE, CO₂- ENRICHMENT, GROWTH, PHOTOSYNTHESIS, RESPONSES, SOYBEAN LEAVES, YIELD

1913

Rabha, B.K., and D.C. Uprety. 1998. Effects of elevated CO₂ and moisture stress on *Brassica juncea*. *Photosynthetica* 35(4):597-602.

The interactive effect of elevated CO₂ (EC) and moisture stress (MS) on

Brassica juncea cv. Pusa Bold was studied using open- top chambers. The EC markedly increased net photosynthetic rate and internal CO₂ concentration and reduced variable and maximal chlorophyll fluorescence. Under MS, EC increased water potential and relative water content, and reduced transpiration rate. The greater allocation of biomass to the roots, which serve as a strong sink for assimilated carbon under EC, helped in better root growth.

KEYWORDS: GROWTH, PHOTOSYNTHESIS, RESPONSES

1914

Raddatz, R.L., and C.F. Shaykewich. 1998. Impact of warm summers on the actual evapotranspiration from spring wheat grown on the eastern Canadian prairies. *Canadian Journal of Soil Science* 78(1):171-179.

How do warm summers (June-July-August) influence the actual evapotranspiration totals from cropped land sown to spring wheat on the eastern Canadian Prairies? The eastern Prairies is a semi-arid region where over 60% of the land is cultivated. Over a third of the cropped land is usually sown to spring wheat. A comparison of mean summer temperatures and modelled evapotranspiration, for the years 1988 to 1996, demonstrated that with the current environmental conditions and farming practices, warm summers have lower actual evapotranspiration totals from spring wheat than cool summers. The average daily actual evapotranspiration rate is generally higher in years with higher mean summer temperatures; however, the crop growth- period is shorter. The net effect is lower total actual evapotranspiration from spring wheat. This suggests that climate warming on the eastern Canadian Prairies, if the current trend continues and all other factors remain equal, will reduce, on average, the total actual evapotranspiration from spring wheat. A reduction in the growth-period actual evapotranspiration from lands sown to spring wheat will likely decrease the total actual evapotranspiration for the entire warm season as growth-period evapotranspiration currently makes up about three-quarters of the seasonal total. However, the magnitude and timing of the reduction is far from certain. The consequence for agriculture may be a reduction in the average spring wheat yield because yield is positively correlated with the actual evapotranspiration total from the crop.

KEYWORDS: AIR CO-2 ENRICHMENT, ENERGY-BALANCE, MODELS, WATER-USE

1915

Radoglou, K.M., P. Aphalo, and P.G. Jarvis. 1992. Response of photosynthesis, stomatal conductance and water-use efficiency to elevated CO₂ and nutrient supply in acclimated seedlings of *Phaseolus vulgaris* L. *Annals of Botany* 70(3):257-264.

KEYWORDS: ACCUMULATION, ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, GROWTH, INHIBITION, IRRADIANCE, LEAVES, PHOSPHORUS, POPLAR CLONES, RIBULOSE BISPHOSPHATE CARBOXYLASE

1916

Radoglou, K.M., and P.G. Jarvis. 1990. Effects of CO₂ enrichment on 4 poplar clones .1. Growth and leaf anatomy. *Annals of Botany* 65(6):617-626.

1917

Radoglou, K.M., and P.G. Jarvis. 1990. Effects of CO₂ enrichment on 4 poplar clones .2. Leaf surface- properties. *Annals of Botany* 65(6):627-632.

1918

Radoglou, K.M., and P.G. Jarvis. 1992. The effects of CO₂ enrichment and nutrient supply on growth- morphology and anatomy of *Phaseolus vulgaris* L seedlings. *Annals of Botany* 70(3):245-256.

KEYWORDS: AREA, ATMOSPHERIC CARBON-DIOXIDE, FORESTS, LEAF ANATOMY, LEAVES, MINERAL NUTRITION, N,N-DIMETHYLFORMAMIDE, PHOTOSYNTHESIS, PLANTS, POPLAR CLONES

1919

Radoglou, K.M., and P.G. Jarvis. 1993. Effects of atmospheric CO₂ enrichment on early growth of vicia- faba, a plant with large cotyledons. *Plant, Cell and Environment* 16(1):93-98.

Seedlings of *Vicia faba* L. were grown in open-top growth chambers at present (P=350 $\mu\text{mol-1}$) and at elevated (E=700 $\mu\text{mol-1}$) atmospheric CO₂ concentration. The effects Of CO₂ enrichment on the first phase of growth after germination were examined over 45d. There were no positive effects Of CO₂ enrichment on growth of the seedlings during this early phase. No differences were observed in leaf area or in total dry weight. No differences were found in morphology or anatomy of the leaves. The numbers of stomatal and epidermal cells, thickness of leaf, of epidermis and of mesophyll cell-layers were unaffected by CO₂ enrichment. Also, no differences were observed in leaf concentrations of chlorophyll, reducing carbohydrates or starch. These results contrast markedly with results from similar experiments on poplar hybrids and *Phaseolus vulgaris* obtained in the same growth facility. It seems that the initial growth is under internal control such that the atmospheric CO₂ concentration has no effects. The lack of response in this case may be attributed to the presence and longevity of the large cotyledons which provided available substrate for growth.

KEYWORDS: POPLAR CLONES

1920

Rafarel, C.R., T.W. Ashenden, and T.M. Roberts. 1995. An improved Solardome system for exposing plants to elevated CO₂ and temperature. *New Phytologist* 131(4):481-490.

Ventilated Solardomes (hemispherical glasshouses) have been used for 20 yr for studying the effects of gaseous pollutants on plants. This paper describes a computer-operated facility for studying the effects of CO₂ x temperature regimes on plants. The eight chambers were set up for factorial design experiments - with two levels of CO₂ (ambient and ambient+340 ppmv), two levels of temperature (ambient and 3 degrees C tracked continuously above ambient) and two replicates of each CO(2)xtemperature treatment. Monitoring of environmental conditions within the chambers over a 2 yr period has shown highly effective control of CO₂ and temperature regimes. Even with high-quality and u.v.-B transmitting glass, the irradiance in the PAR region was reduced by 18 % within the domes. Variation in temperature across the radii of the domes increased with higher photosynthetic photon flux density (PPFD). Vapour pressure deficits (VPDs) in the ambient temperature domes compared well with outside conditions but were higher in the elevated temperature domes. The watering regime within the domes affected intermittently the relationship between 'dome' and 'outside' VPDs. The Solardome facility has been used extensively for studies of the impacts of climate change within the UK Programme on Terrestrial Initiative on Global Environmental Research (TIGER).

KEYWORDS: AIR-POLLUTION, CHAMBERS, ECOSYSTEMS, EXPOSURE, FIELD, OZONE, POLLUTANTS, STRESS, TREES

1921

Raich, J.W., and A. Tufekciogul. 2000. Vegetation and soil respiration: Correlations and controls. *Biogeochemistry* 48(1):71-90.

Soil respiration rates vary significantly among major plant biomes, suggesting that vegetation type influences the rate of soil respiration. However, correlations among climatic factors, vegetation distributions, and soil respiration rates make cause-effect arguments difficult. Vegetation may affect soil respiration by influencing soil microclimate and structure, the quantity of detritus supplied to the soil, the quality of that detritus, and the overall rate of root respiration. At the global scale, soil respiration rates correlate positively with litterfall rates in forests, as previously reported, and with aboveground net primary productivity in grasslands, providing evidence of the importance of detritus supply. To determine the direction and magnitude of the effect of vegetation type on soil respiration, we collated data from published studies where soil respiration rates were measured simultaneously in two or more plant communities. We found no predictable differences in soil respiration between cropped and vegetation-free soils, between forested and cropped soils, or between grassland and cropped soils, possibly due to the diversity of crops and cropping systems included. Factors such as temperature, moisture availability, and substrate properties that simultaneously influence the production and consumption of organic matter are more important in controlling the overall rate of soil respiration than is vegetation type in most cases. However, coniferous forests had similar to 10% lower rates of soil respiration than did adjacent broad-leaved forests growing on the same soil type, and grasslands had, on average, similar to 20% higher soil respiration rates than did comparable forest stands, demonstrating that vegetation type does in some cases significantly affect rates of soil respiration.

KEYWORDS: BOREAL FOREST ECOSYSTEMS, CARBON-DIOXIDE EVOLUTION, CLIMATIC CHANGE, LAND-USE, MAINTENANCE RESPIRATION, NITROGEN MINERALIZATION, PINE PLANTATIONS, PRIMARY PRODUCTIVITY, ROOT RESPIRATION, SEASONAL PATTERN

1922

Raiesi, F.G., and P. Buurman. 1998. Effects of CO₂ enrichment on quality of leaf litter and on soil C dynamics in a Mediterranean forest ecosystem. *Fresenius Environmental Bulletin* 7(5A-6A):429-436.

We discuss the effect of long-term elevated CO₂ on quality and decomposability of litter from mature trees, and its influence on soil organic matter (SOM) dynamics by evaluating the available data from mineral CO₂ springs in Central Italy. Results from the vegetation around these natural CO₂ springs demonstrate that elevated CO₂ did not affect litter quality. Consequently, C and N mineralization rates remained unaffected by CO₂ level. However, there were significant differences in litter quality and decomposition between species. Results from soil analysis indicate that elevated CO₂ increased the total organic C content and C pool sizes in the F layer, but not in HA and 0-10 cm layers. Neither were soil N, C/N ratio and the decomposition of SOM affected by elevated CO₂. Soil N mineralization in the forest floor seems to be enhanced by CO₂ enrichment.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, BIOSPHERE, DECOMPOSITION RATES, ELEVATED CO₂, GRASSLAND, RESPONSES

1923

Ranasinghe, S., and G. Taylor. 1996. Mechanism for increased leaf growth in elevated CO₂. *Journal of Experimental Botany* 47(296):349-358.

The effect of exposure to elevated CO₂ on the processes of leaf cell

production and leaf cell expansion was studied using primary leaves of *Phaseolus vulgaris* L. Cell division and expansion were separated temporally by exposing seedlings to dim red light for 10 d (when leaf cell division was completed) followed by exposure to bright white light for 14 d (when leaf growth was entirely dependent on cell expansion). When plants were exposed to elevated CO₂ during the phase of cell expansion, epidermal cell size and leaf area development were stimulated. Three pieces of evidence suggest that this occurred as a result of increased cell wall loosening and extensibility, (i) cell wall extensibility (WEx, measured as tensiometric extension using an Instron) was significantly increased, (ii) cell wall yield turgor (Y, MPa) was reduced and (iii) xyloglucan endotransglycosylase (XET) enzyme activity was significantly increased. When plants were exposed to elevated CO₂ during the phase of cell division, the number of epidermal cells was increased whilst final cell size was significantly reduced and this was associated with reduced final leaf area, WEx and XET activity. When plants were exposed to elevated CO₂ during both phases of cell division and expansion, leaf area development was not affected. For this treatment, however, the number of epidermal cells was increased, but cell expansion was inhibited, despite exposure to elevated CO₂ during the expansion phase. Assessments were also made of the spatial patterns of WEx across the expanding leaf lamina and the data suggest that exposure to elevated CO₂ during the phase of leaf expansion may lead to enhanced extensibility particularly at basal leaf margins which may result in altered leaf shape. The data show that both cell production and expansion were stimulated by elevated CO₂, but that leaf growth was only enhanced by exposure to elevated CO₂ in the cell expansion phase of leaf development. Increased leaf cell expansion is, therefore, an important mechanism for enhanced leaf growth in elevated CO₂, whilst the importance of increased leaf cell production in elevated CO₂ remains to be elucidated.

KEYWORDS: CELL, ELONGATION, ENRICHMENT, EXPANSION, WALL EXTENSIBILITY, XYLOGLUCAN ENDOTRANSGLYCOSYLASE ACTIVITY

1924

Randerson, J.T., M.V. Thompson, and C.B. Field. 1999. Linking C-13-based estimates of land and ocean sinks with predictions of carbon storage from CO₂ fertilization of plant growth. *Tellus Series B-Chemical and Physical Meteorology* 51(3):668-678.

The residence times of carbon in plants, litter, and soils are required for partitioning land and ocean sinks using measurements of atmospheric delta(13)CO(2) and also for estimating terrestrial carbon storage in response to net primary production (NPP) stimulation by elevated levels of atmospheric CO₂. While C-13-based calculations of the land sink decline with increasing estimates of terrestrial carbon residence times (through the fossil fuel-induced isotopic disequilibrium term in equations describing the global atmospheric budgets of (CO₂)-C-13 and CO₂), estimates of land sinks based on CO₂ fertilization of plant growth are directly proportional to carbon residence times. Here we used a single model of terrestrial carbon turnover, the Carnegie Ames- Stanford Approach (CASA) biogeochemical model, to simultaneously estimate 1984-1990 terrestrial carbon storage using both approaches. Our goal was to identify the fraction of the (CO₂)-C-13-based land sink attributable to CO₂ fertilization. Uptake from CO₂ fertilization was calculated using a beta factor of 0.46 to describe the response of NPP to increasing concentrations of atmospheric CO₂ from 1765 to 1990. Given commonly used parameters in the C-13-based sink calculation and assuming a deforestation flux of 0.8 Pg C/yr, CO₂ fertilization accounts for 54% of the missing terrestrial carbon sink from 1984 to 1990. CO₂ fertilization can account for all of the missing terrestrial sink only when the terrestrial mean residence time (MRT) and the land isodisequilibrium forcing are greater than many recent estimates.

KEYWORDS: ATMOSPHERIC CO₂, C-13, C-13/C-12 RATIO,

1925

Randlett, D.L., D.R. Zak, K.S. Pregitzer, and P.S. Curtis. 1996. Elevated atmospheric carbon dioxide and leaf litter chemistry: Influences on microbial respiration and net nitrogen mineralization. *Soil Science Society of America Journal* 60(5):1571-1577.

Elevated atmospheric CO₂ has the potential to influence rates of C and N cycling in terrestrial ecosystems by altering plant litter chemistry and slowing rates of organic matter decomposition. We tested the hypothesis that the chemistry of leaf litter produced at elevated CO₂ would slow C and N transformations in soil. Soils were amended with *Populus* leaf litter produced under two levels of atmospheric CO₂ (ambient and twice-ambient) and soil N availability (low and high). Kinetic parameters for microbial respiration and net N mineralization were determined on soil with and without litter during a 32-wk lab incubation. Product accumulation curves for CO₂-C and inorganic N were fit to a first order rate equation [$y = A(1 - e^{-(kt)})$] using nonlinear regression analyses. Although CO₂ treatment affected soluble sugar concentration in leaf litter (ambient = 120 g kg⁻¹, elevated = 130 g kg⁻¹), it did not affect starch concentration or C/N ratio. Microbial respiration, microbial biomass, and leaf litter C/N ratio were affected by soil N availability but not by atmospheric CO₂. Net N mineralization was a linear function of time and was not significantly different for leaves grown at ambient (50 mg N kg⁻¹) and elevated CO₂ (35 mg N kg⁻¹). Consequently, we found no evidence for the hypothesis that leaf litter produced at elevated atmospheric CO₂ will dampen the rates of C and N cycling in soil.

KEYWORDS: CO₂, DECOMPOSITION, EFFICIENCY, ENRICHMENT, GROWTH, PRODUCTIVITY, RESPONSES, SEEDLINGS, SOIL-NITROGEN, TERRESTRIAL ECOSYSTEMS

1926

Rao, M.V., and L.J. Dekok. 1994. Interactive effects of high CO₂ and SO₂ on growth and antioxidant levels in wheat. *Phyton-Annales Rei Botanicae* 34(2):279-290.

The impact of elevated CO₂ and/or SO₂ on the growth and antioxidant levels of wheat (*Triticum aestivum* L. cv. Urban) plants has been studied. High CO₂ (0.7 ml l⁻¹) significantly enhanced shoot biomass and photosynthetic capacity, while exposure to SO₂ (0.14 ml l⁻¹) resulted in a decreased shoot biomass and in an injured photosynthetic apparatus, illustrated by a loss of chlorophyll and a decreased ratio of variable to maximal fluorescence ($F(v)/F(m)$) and $A(max)$. However, combined exposure of plants to high CO₂ and SO₂ eliminated the negative effects of SO₂. Sulfate accumulation was almost equal in plants exposed to SO₂ and, high CO₂ and SO₂. A significant increase in ascorbate, glutathione and their redox state was observed in plants exposed to high CO₂ and SO₂, compared to that of plants exposed to solely SO₂. The absence of the negative effects of SO₂ in the presence of high CO₂ might be related to a high redox state of ascorbate and glutathione. Abbreviations: $A(max)$, maximum rate of oxygen evolution at saturated light and CO₂ ($\mu\text{mol m}^{-2} \text{s}^{-1}$); ASA, reduced ascorbic acid; DHA, dehydroascorbic acid; $F(m)$, maximum emission of photosystem-II chlorophyll fluorescence; $F(v)$, variable component of $F(m)$; GSH, reduced glutathione; GSSG, oxidized glutathione.

1927

Rao, M.V., B.A. Hale, and D.P. Ormrod. 1995. Amelioration of ozone-induced oxidative damage in wheat plants grown under high-carbon dioxide - role of antioxidant enzymes. *Plant Physiology*

109(2):421-432.

O₃-induced changes in growth, oxidative damage to protein, and specific activities of certain antioxidant enzymes were investigated in wheat plants (*Triticum aestivum* L. cv Roblin) grown under ambient or high CO₂. High CO₂ enhanced shoot biomass of wheat plants, whereas O₃ exposure decreased shoot biomass. The shoot biomass was relatively unaffected in plants grown under a combination of high CO₂ and O₃. O₃ exposure under ambient CO₂ decreased photosynthetic pigments, soluble proteins, and ribulose-1,5-bisphosphate carboxylase/oxygenase protein and enhanced oxidative damage to proteins, but these effects were not observed in plants exposed to O₃ under high CO₂. O₃ exposure initially enhanced the specific activities of superoxide dismutase, peroxidase, glutathione reductase, and ascorbate peroxidase irrespective of growth in ambient or high CO₂. However, the specific activities decreased in plants with prolonged exposure to O₃ under ambient CO₂ but not in plants exposed to O₃ under high CO₂. Native gels revealed preferential changes in the isoform composition of superoxide dismutase, peroxidases, and ascorbate peroxidase of plants grown under a combination of high CO₂ and O₃. Furthermore, growth under high CO₂ and O₃ led to the synthesis of one new isoform of glutathione reductase. This could explain why plants grown under a combination of high CO₂ and O₃ are capable of resisting O₃-induced damage to growth and proteins compared to plants exposed to O₃ under ambient CO₂.

KEYWORDS: AIR- POLLUTANTS, ASCORBATE PEROXIDASE, ATMOSPHERIC CO₂ CONCENTRATION, B RADIATION, ELEVATED CO₂, ENRICHMENT, PHOTOSYNTHETIC RESPONSE, PROTEINS, SULFUR-DIOXIDE, SUPEROXIDE-DISMUTASE

1928

Rastetter, E.B. 1996. Validating models of ecosystem response to global change. *BioScience* 46(3):190-198.

KEYWORDS: BIOMASS, CARBON BUDGET, CLIMATE, ELEVATED CO₂, PHOTOSYNTHESIS, TEMPERATURE, TUNDRA

1929

Rastetter, E.B., and G.R. Shaver. 1992. A model of multiple-element limitation for acclimating vegetation. *Ecology* 73(4):1157-1174.

In this paper we present a simple model of multiple-element limitation of plant production and biomass accumulation. The primary aim of this model is to develop a theoretical framework for examining multiple-element limitation vs. single-element limitation and for examining the relationship between short-term and long-term responses to changes in element availability. In the model we assume that there is an "optimal" ratio of mineral elements in vegetation biomass, and that the vegetation continually adjusts its relative element uptake capacities to compensate for shifts away from this optimum. We examine the responses of this model to changes in element availability in the plant environment, where "availability" is defined either as fixed concentrations of non-depletable elements or as fixed replenishment rates of depletable elements. The model results suggest that the nature of the controls on element availability has a major impact on whether single- or multiple-element limitation prevails, even when plants can acclimate so as to maintain an "optimal" nutritional balance. Single-element limitation occurs when the replenishment rate of an essential element to the available pool is limited and sustainable plant uptake of that element equals the replenishment rate. Furthermore, when single-element limitation prevails, there is little or no correlation between short-term responses to a change in element availability and long-term, equilibrium responses. In general, previous experimental studies and models of plant growth in response to changes in relative availability of multiple, essential elements have either not specified how those resources are controlled, or have examined only one

type of control. Our results help to explain the diversity of results of past studies of multiple-element limitation, suggest some improvements in experimental design for future studies, and have important implications for the extrapolation of the results of controlled experiments to field situations.

KEYWORDS: CO₂-ENRICHMENT, COMPETITION, ECOSYSTEMS, EFFICIENCY, GROWTH, NITROGEN-AVAILABILITY, PHOTOSYNTHESIS, PLANTS, TAIGA TREES, TEMPERATURE

1930

Ratanachinakorn, B., A. Klieber, and D.H. Simons. 1997. Effect of short-term controlled atmospheres and maturity on ripening and eating quality of tomatoes. *Postharvest Biology and Technology* 11(3):149-154.

Mature green, breaker, and pink 'Bermuda' tomatoes (*Lycopersicon esculentum* Mill.) were treated in air, 0.5% O₂ for 1 day, or 80% CO₂ for 1 or 2 days at 22 degrees C before ripening in air at 22 degrees C. Headspace ethanol (EtOH) and acetaldehyde (AA), soluble solids (SS), titratable acidity (TA), and pH were measured, and sensory quality was determined using descriptive analysis with a trained panel. Some ripening delay of 1-2 days was observed due to low O₂ and 2 days of high CO₂. EtOH and AA production increased more with increasing fruit maturity and with low O₂ at these maturities; both volatiles dissipated to trace amounts before fruit were eating ripe in all treatments. Aroma and taste were not enhanced by any treatment/ripeness combinations, although 80% CO₂ for 2 days marginally increased the sweetness and blandness of the fruit. Soluble solids, titratable acidity and pH were not different between treatments or ripening stages. (C) 1997 Elsevier Science B.V.

KEYWORDS: ACETALDEHYDE VAPOR, ANAEROBIC CONDITIONS, EXPRESSION, FRUIT, ORANGES, POSTHARVEST APPLICATION, STORAGE, VOLATILES

1931

Rathgeber, C., J. Guiot, P. Roche, and L. Tessier. 1999. *Quercus humilis* increase of productivity in the Mediterranean area. *Annals of Forest Science* 56(3):211-219.

Several recent studies have shown an increasing long-term growth trend for various forest tree species in western Europe. Nevertheless such studies have not yet, been performed in Mediterranean Europe. The aim of this work is to analyse changes in productivity of some Mediterranean forest ecosystems compared with other mediterranean forest ecosystems. Sixteen *Quercus humilis* (Miller) populations were sampled in south-east France. Tree ring widths were measured for each tree according to three radius, and annual basal area increments were calculated. Two growth indexes (IP and IC) were calculated with two different standardization techniques, in order to remove age and interstation productivity effects. From the IP and IC indexes we can see that there was a productivity increase during the last century, this increase being evaluated at 100 % (IC index). These results indicate that the Mediterranean forest ecosystems have shown a high productivity increase over the last century, as have the mediterranean forest ecosystems. The best hypothesis to explain this increasing long-term growth trend is a direct CO₂ fertilization along with N deposition fertilization. ((C) Inra/Elsevier, Paris.).

KEYWORDS: ATMOSPHERIC CO₂, CARBON DIOXIDE, CLIMATE, ENERGY-PRODUCTION, FERTILIZATION, FOREST ECOSYSTEMS, GROWTH-RESPONSES, NORTHEASTERN FRANCE, TREE-RING CHRONOLOGY, TRENDS

1932

Rattray, E.A.S., E. Paterson, and K. Killham. 1995. Characterization of the dynamics of C-partitioning within lolium-perenne and to the rhizosphere microbial biomass using C-14 pulse-chase. *Biology and Fertility of Soils* 19(4):280-286.

The dynamics of C partitioning with *Lolium perenne* and its associated rhizosphere was investigated in plant-soil microcosms using C-14 pulse-chase labelling. The CO₂(C-14) pulse was introduced into the shoot chamber and the plants allowed to assimilate the label for a fixed period. The microcosm design facilitated independent monitoring of shoot and root/soil respiration during the chase period. Partitioning between above- and below-ground pools was determined between 30 min and 168 h after the pulse, and the distribution was found to vary with the length of the chase period. Initially (30 min after the pulse), C-14 was predominantly (99%) in the shoot biomass and declined thereafter. The results indicate that translocation of recent photoassimilate is rapid, with C-14 detected below ground within 30 min of pulse application. The translocation rate of C-14 below ground was maximal (6.2% h⁻¹) between 30 min and 3h after the pulse, with greatest incorporation into the microbial biomass detected at 3 h. After 3 h, the microbial biomass C-14 pool accounted for 74% of the total C-14 rhizosphere pool. By 24 h, approximately 30% of C-14 assimilate had been translocated below ground; thereafter C-14 translocation was greatly reduced. Partitioning of recent assimilate changed with increasing CO₂ concentration. The proportion of C-14 translocated below ground almost doubled from 17.76% at the ambient atmospheric CO₂ concentration (450 ppm) to 33.73% at 750 ppm CO₂ concentration. More specifically, these changes occurred in the root biomass and the total rhizosphere pools, with two- and threefold C-14 increases at an elevated CO₂ concentration compared to ambient, respectively. The pulse- labelling strategy developed in this study provided sufficient sensitivity to determine perturbations in C dynamics in *L. perenne*, in particular rhizosphere C pools, in response to an elevated atmospheric CO₂ concentration.

KEYWORDS: ATMOSPHERIC CO₂, CARBON FLOW, FIELD PLOTS, GROWTH-RESPONSE, NITROGEN, PLANTS, ROOTS, SANDY LOAM, SOIL, WHEAT

1933

Raveh, E., M. Gersani, and P.S. Nobel. 1995. Co₂ uptake and fluorescence responses for a shade-tolerant cactus *hylocereus-undatus* under current and doubled co₂ concentrations. *Physiologia Plantarum* 93(3):505-511.

Hylocereus undatus (Haworth) Britton and Rose growing in controlled environment chambers at 370 and 740 $\mu\text{mol CO}_2 \text{ mol}^{-1} \text{ air}$ showed a C₃ acid metabolism (CAM) pattern of CO₂ uptake, with 34% more total daily CO₂ uptake under the doubled CO₂ concentration and most of the increase occurring in the late afternoon. For both CO₂ concentrations, 90% of the maximal daily CO₂ uptake occurred at a total daily photosynthetic photon flux density (PPFD) of only 10 $\text{mol m}^{-2} \text{ day}^{-1}$ and the best day/night air temperatures were 25/15 degrees C. Enhancement of the daily net CO₂ uptake by doubling the CO₂ concentration was greater under the highest PPFD (30 $\text{mol m}^{-2} \text{ day}^{-1}$) and extreme day/night air temperatures (15/5 and 45/35 degrees C). After 24 days of drought, daily CO₂ uptake under 370 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ was 25% of that under 740 $\mu\text{mol CO}_2 \text{ mol}^{-1}$. The ratio of variable to maximal chlorophyll fluorescence (F_v/F_m) decreased as the PPFD was raised above 5 $\text{mol m}^{-2} \text{ day}^{-1}$, at extreme day/night temperatures and during drought, suggesting that stress occurred under these conditions. F_v/F_m was higher under the doubled CO₂ concentration, indicating that the current CO₂ concentration was apparently limiting for photosynthesis. Thus net CO₂ uptake by the shade-tolerant *H. undatus*, the photosynthetic efficiency of which was greatest at low PPFDs, showed a positive response to doubling the CO₂ concentration, especially under stressful environmental conditions.

KEYWORDS: AGAVE-VILMORINIANA, CARBON DIOXIDE, CRASSULACEAN ACID METABOLISM, ELEVATED CO₂, ENRICHMENT, EXCHANGE, GROWTH, LEAVES, OPUNTIA FICUS INDICA, PLANT

1934

Raven, J.A. 1994. Carbon fixation and carbon availability in marine-phytoplankton. *Photosynthesis Research* 39(3):259-273.

It is widely believed that inorganic C does not limit the rate of short-term photosynthesis, the net productivity, or the maximum biomass, of marine phytoplankton. This lack of inorganic C restriction is less widely believed to hold for phytoplankton in many low alkalinity freshwaters or for seaweed in nutrient-enriched rock pools. These views are examined in the context of the physical chemistry of the inorganic C system in natural waters and of the ways in which various taxa of phytoplankton deal with inorganic C and discriminate between C-12 and C-13. Using this information to interpret data obtained in the ocean or in freshwater suggests that short-term photosynthesis, production rate, and achieved biomass, of phytoplankton are rarely limited by inorganic C supply but, rather, that the widely suggested factors of limited light, nitrogen or phosphorus supply are the resource inputs which restrict productivity. Global change, by increasing atmospheric CO₂ partial pressure and global mean temperatures, is likely to increase the mean CO₂ concentration in the atmosphere, but the corresponding change in the oceans will be much less. There are, however, genotypic differences in the handling of inorganic C among the diversity of marine phytoplankton, and in impact on use of limiting nutrients, so increases in the mean CO₂ and HCO₃⁻ concentrations in surface ocean waters could cause changes in species composition. However, the rarity of inorganic C limitation of marine phytoplankton short-term photosynthesis, net productivity, or the maximum biomass, in today's ocean means that global change is unlikely to increase these three values in the ocean.

KEYWORDS: ATMOSPHERIC CO₂, DELTA C 13, GROWTH-RATES, ICE CORE, INORGANIC CARBON, NATURAL ABUNDANCE, PLANTS, PRODUCTIVITY, SURFACE OCEAN, TEMPERATURE

1935

Rawson, H.M. 1992. Plant-responses to temperature under conditions of elevated CO₂. *Australian Journal of Botany* 40(4-5):473-490.

A literature survey of the interactive effects of CO₂ enrichment and temperature on plant development and growth, indicated that the responses cannot be interpreted within a simple framework. For example, although plant development is generally accelerated by increased temperature, CO₂ enrichment can accelerate it even further in some instances, or CO₂ enrichment may have neutral or even retarding effects in other cases. Where the temperature and CO₂ effects are additive, it is argued that CO₂ is operating in the same way as radiation to reduce a carbon limitation. If this were true, CO₂ enrichment would be most likely to accelerate development in tropical regions during the low-radiation monsoon season. Similarly, while it would be expected that CO₂-enrichment would have increasingly enhancing effects with increasing temperature on phytomass growth, this is not invariably the case. In extreme examples which followed the expected trend, plants grown in twice-normal CO₂-enriched atmospheres performed progressively better than those grown at current levels of CO₂ by 8.7% for every 1-degrees-C rise in temperature. However, the difference between the two CO₂ treatments more commonly increased by only around 2% for every 1-degrees-C rise in temperature. Of examples examined, both sunflower and nodulated cowpea showed the reverse response to temperature, while non-nodulated cowpea, supplied with luxuriant levels of nutrition, showed no interaction with temperature but a strong interaction between CO₂ and radiation. Other aspects of the

environment such as nutrition and radiation strongly modify the responses to temperature. It is also clear that plant factors such as stage of development can alter the response to CO₂. Long-term studies with several species are required which will take into account many environmental variables within a realistic envelope. One methodology for doing this is presented. There was no evidence among species that responses to CO₂ arise through any consistent change in morphology such as via increased branching or increased leaf number. Plant plasticity is such that responses can be expressed in a variety of ways determined by other environmental variables.

KEYWORDS: AIR-TEMPERATURE, ATMOSPHERIC CO₂, CARBON-DIOXIDE ENRICHMENT, KUDZU PUERARIA-LOBATA, LEAF EXPANSION, SEED YIELD, SPRING WHEAT, WATER-USE, WINTER-WHEAT, YIELD COMPONENTS

1936

Rawson, H.M. 1995. Yield responses of 2 wheat genotypes to carbon-dioxide and temperature in-field studies using temperature-gradient tunnels. *Australian Journal of Plant Physiology* 22(1):23-32.

Clear, plastic-coated, temperature gradient tunnels (TGTs), 8 X 1.25 X 1.25 m were designed and built to examine how temperature and CO₂ affect the yield of wheat in the field. Each of the three modules of each TGT was maintained at a different temperature above the ambient temperature using solar heating during the day and electric heating at night. The maximum day-time increment above ambient for the warmest module was 5 degrees C and full-season averages were close to 2 degrees C. TGTs were paired, with air in one being enriched to 700 μ mol L⁻¹ CO₂, and in the other being maintained at ambient CO₂. Crops were planted in the TGTs at two sites in either summer (December) or winter (April and July) and they remained there until maturity. CO₂ enrichment increased the yield in summer plantings by up to 36%. In winter plantings, with mean temperatures between sowing and anthesis of around 10 degrees C, the responses to CO₂ were small averaging only 7% (range 1-12%). Though yield declined with increasing temperature in the TGTs in summer, there was a clear trend for an increasing response to CO₂ at these higher temperatures, i.e. yield declined less. In summer, there was no convincing evidence for a different relative response to CO₂ in two isolines which differed in maturity date, though the later line yielded more under the highest temperature regime (mean of 22-24 degrees C between sowing and anthesis). In winter there was a strong trend for the isoline requiring less vernalisation to respond more to CO₂. It is suggested that early progress towards flowering might predispose wheat to a greater CO₂ response. Overall, the data indicated that the positive response to CO₂ in grain yield is likely to increase at approximately 1.8% per 1 degrees C in wheat crops that are not limited by water. Extrapolation indicated that the temperature at which there was no response to CO₂ was 5 degrees C. All yield responses reflected biomass responses as harvest index was unchanged by CO₂.

KEYWORDS: ATMOSPHERIC CO₂ ENRICHMENT, CULTIVAR, ELEVATED CO₂, PHOTOPERIOD, PHOTOSYNTHESIS, PLANT GROWTH, POA-PRATENSIS, PRODUCTIVITY, STRESS, WATER

1937

Read, J.J., and J.A. Morgan. 1996. Growth and partitioning in *Pascopyrum smithii* (C-3) and *Bouteloua gracilis* (C-4) as influenced by carbon dioxide and temperature. *Annals of Botany* 77(5):487-496.

This study investigated how CO₂ and temperature affect dry weight (d.wt) accumulation, total nonstructural carbohydrate (TNC) concentration, and partitioning of C and N among organs of two important grasses of the shortgrass steppe, *Pascopyrum smithii* Rydb. (C-3) and *Bouteloua gracilis* (H.B.K.) Lag. ex Steud. (C-4). Treatment combinations comprised two temperatures (20 and 35 degrees C) at two

concentrations of CO₂ (380 and 750 $\mu\text{mol mol}^{-1}$), and two additional temperatures of 25 and 30 degrees C at 750 $\mu\text{mol mol}^{-1}$ CO₂. Plants were maintained under favourable nutrient and soil moisture and harvested following 21, 35, and 49 d of treatment. CO₂-induced growth enhancements were greatest at temperatures considered favourable for growth of these grasses. Compared to growth at 380 $\mu\text{mol mol}^{-1}$ CO₂, final d.wt of CO₂-enriched *P. smithii* increased 84% at 20 degrees C but only 4% at 35 degrees C. Final d.wt of *B. gracilis* was unaffected by CO₂ at 20 degrees C, but was enhanced by 28% at 35 degrees C. Root:shoot ratios remained relatively constant across CO₂ levels, but increased in *P. smithii* with reduction in temperature. These partitioning results were adequately explained by the theory of balanced root and shoot activity. Favourable growth temperatures led to CO₂-induced accumulations of TNC in leaves of both species, and in stems of *P. smithii*, which generally reflected responses of above-ground d.wt partitioning to CO₂. However, CO₂-induced decreases in plant tissue N concentrations were more evident for *P. smithii*. Roots of CO₂-enriched *P. smithii* had greater total N content at 20 degrees C, an allocation of N below-ground that may be an especially important adaptation for C-3 plants. Tissue N contents of *B. gracilis* were unaffected by CO₂. Results suggest CO₂ enrichment may lead to reduced N requirements for growth in C-3 plants and lower shoot N concentration, especially at favourable growth temperatures. (C) 1996 Annals of Botany Company

KEYWORDS: ATMOSPHERIC CO₂ CONCENTRATIONS, BIOMASS, ENRICHMENT, MODEL, NITROGEN, RESPONSES

1938

Read, J.J., J.A. Morgan, N.J. Chatterton, and P.A. Harrison. 1997. Gas exchange and carbohydrate and nitrogen concentrations in leaves of *Paspopyrum smithii* (C-3) and *Bouteloua gracilis* (C-4) at different carbon dioxide concentrations and temperatures. *Annals of Botany* 79(2):197-206.

Paspopyrum smithii (C-3) and *Bouteloua gracilis* (C-4) are important forage grasses native to the Colorado shortgrass steppe. This study investigated photosynthetic responses of these grasses to long-term CO₂ enrichment and temperature in relation to leaf nonstructural carbohydrate (TNC) and [N]. Glasshouse-grown seedlings were transferred to growth chambers and grown for 49 d at two CO₂ concentrations (380 and 750 $\mu\text{mol mol}^{-1}$) at 20 and 35 degrees C, and two additional temperatures (25 and 30 degrees C) at 750 $\mu\text{mol mol}^{-1}$ CO₂. Leaf CO₂ exchange rate (CER) was measured at a plant's respective growth temperature and at two CO₂ concentrations of approx. 380 and 700 $\mu\text{mol mol}^{-1}$. Long-term CO₂ enrichment stimulated CER in both species, although the response was greater in the CER *P. smithii*. Doubling the [CO₂] from 380 to 750 $\mu\text{mol mol}^{-1}$ stimulated CER of *P. smithii* slightly more in plants grown and measured at 30 degrees C compared to plants grown at 20, 25 or 35 degrees C. CO₂-enriched plants sometimes exhibited lower CER when compared to ambient-grown controls measured at the same [CO₂], indicating photosynthetic acclimation to CO₂ growth regime. In *P. smithii*, such reductions in CER were associated with increases in TNC and specific leaf mass, reductions in leaf [N] and, in one instance, a reduction in leaf conductance compared to controls. In *B. gracilis*, photosynthetic acclimation was observed more often, but significant changes in leaf metabolite levels from growth at different [CO₂] were generally less evident. Temperatures considered optimal for growth (C-3: 20 degrees C; C-4: 35 degrees C) sometimes led to CO₂-induced accumulations of TNC in both species, with starch accumulating in the leaves of both species, and fructans accumulating only in *P. smithii*. Photosynthesis of both species is likely to be enhanced in future CO₂-enriched and warmer environments, although responses will sometimes be attenuated by acclimation. (C) 1997 Annals of Botany Company.

KEYWORDS: ACCLIMATION, ACCUMULATION, ATMOSPHERIC CO₂ CONCENTRATIONS, BOUTELOUA-GRACILIS, COOL

TEMPERATURES, ELEVATED CO₂, GROWTH, PHOTOSYNTHESIS, PLANTS, STARCH

1939

Reddy, A.R., K.R. Reddy, and H.F. Hodges. 1998. Interactive effects of elevated carbon dioxide and growth temperature on photosynthesis in cotton leaves. *Plant Growth Regulation* 26(1):33-40.

Cotton (*Gossypium hirsutum* L., cv DPL 5415) plants were grown in naturally lit environment chambers at day/night temperature regimes of 26/18 (T26/18), 31/23 (T-31/23) and 36/28 degrees C (T-36/28) and CO₂ concentrations of 350 (C-350), 450 (C-450) and 700 $\mu\text{mol mol}^{-1}$ (C-700). Net photosynthesis rates, stomatal conductance, transpiration, RuBP carboxylase activity and the foliar contents of starch and sucrose were measured during different growth stages. Net CO₂ assimilation rates increased with increasing CO₂ and temperature regimes. The enhancement of photosynthesis was from 24 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ (with C-350 and T-26/18) to 41 $\mu\text{mol m}^{-2} \text{ s}^{-1}$ (with C-700 and T-36/28). Stomatal conductance decreased with increasing CO₂ while it increased up to T-31/23 and then declined. The interactive effects of CO₂ and temperature resulted in a 30% decrease in transpiration. Although the leaves grown in elevated CO₂ had high starch and sucrose concentrations, their content decreased with increasing temperature. Increasing temperature from T-26/18 to 36/28 increased RuBP carboxylase activity in the order of 121, 172 and 190 $\mu\text{mol mg}^{-1} \text{ chI h}^{-1}$ at C-350, C-450 and C-700 respectively. Our data suggest that leaf photosynthesis in cotton benefited more from CO₂ enrichment at warm temperatures than at low growth temperature regimes.

KEYWORDS: ACCLIMATION, ACTIVATION, ATMOSPHERIC CO₂, ENRICHMENT, PLANTS, PROTEIN, RATES, RICE

1940

Reddy, K.R., G.H. Davidonis, A.S. Johnson, and B.T. Vinyard. 1999. Temperature regime and carbon dioxide enrichment alter cotton boll development and fiber properties. *Agronomy Journal* 91(5):851-858.

Temperature and atmospheric carbon dioxide concentration [CO₂] affect cotton (*Gossypium hirsutum* L.) growth and development, but the interaction of these two factors on boll and fiber properties has not been studied. An experiment was conducted in naturally lit plant growth chambers to determine the influence of temperature and atmospheric [CO₂] on cotton (cv. DPL-51) boll and fiber growth parameters. Five temperature regimes were evaluated: the 1995 temperature at Mississippi State, MS; the 1995 temperature minus 2 degrees C; and the 1995 temperature plus 2, 5, and 7 degrees C. Daily and seasonal variation and amplitudes were maintained. Atmospheric [CO₂] treatments were 360 (ambient) and 720 $\mu\text{mol L}^{-1}$. Boll number, boll growth, and fiber properties were measured. Boll size and maturation periods decreased as temperature increased. Boll growth increased with temperature to 25 degrees C and then declined at the highest temperature. Boll maturation period, size, and growth rates were not affected by atmospheric [CO₂]. The most temperature-sensitive aspect of cotton development is boll retention. Almost no bolls were retained to maturity at 1995 plus 5 or 7 degrees C, but squares and bolls were continuously produced even at those high temperatures. Therefore, the upper limit for cotton boll survival is 32 degrees C, or 5 degrees C warmer than the 1995 U.S. Mid-South ambient temperatures. The 720 $\mu\text{mol L}^{-1}$ atmospheric [CO₂] had about 40% more squares and bolls across temperatures than the 360 $\mu\text{mol L}^{-1}$ [CO₂]. Fibers were longer when bolls grew at less than optimal temperatures (25 degrees C) for boll growth. As temperature increased, fiber length distributions were more uniform. Fiber fineness and maturity increased linearly with the increase in temperature up to 26 degrees C, but decreased at 32 degrees C. Short-fiber content declined linearly from 17 to 26 degrees C, but was higher at higher temperature.

As for boll growth and developmental parameters, elevated atmospheric [CO₂] did not affect any of the fiber parameters. Changes in temperature, however, had a dramatic effect on boll set and tiber properties. The relationships between temperature and boll growth and developmental rate functions and fiber properties provide the necessary functional parameters to build fiber models under optimum water and nutrient conditions.

KEYWORDS: CROP MANAGEMENT, GROWTH, RAY-FLUORESCENCE SPECTROSCOPY, RICE, SIMULATION-MODEL, SYSTEM

1941

Reddy, K.R., H.F. Hodges, and J.M. McKinion. 1995. Carbon-dioxide and temperature effects on pima cotton development. *Agronomy Journal* 87(5):820-826.

Predicting plant responses to changing atmospheric CO₂ and to the possible global warming are important concerns. Effects of CO₂ on developmental events are poorly documented, as is the interaction of CO₂ and other major climate variables on crop development. The objective of this experiment was to determine the effects of an altered CO₂ environment and interactions of CO₂ and temperature on pima cotton developmental rates. Pima cotton (*Gossypium barbadense* L. cv. S-6) was grown from seed in sun-lit plant growth chambers. Air temperatures were controlled from 20/12 to 40/32 degrees C (day/night) in 5-degree increments. Daytime CO₂ was maintained at 350 or 700 mu L L(-1). In a second experiment, the temperature was maintained at 30/22 degrees C day/night and the plants were grown in 350, 450, or 700 mu L L(-1) CO₂. Days required to develop nodes on the mainstem, days from emergence to first square, number of vegetative and fruiting branches, number of fruiting sites produced, number of bells and squares produced, and number of bells and squares retained by the plants were determined. Rates of mainstem node formation and the time required to produce the first square and first flower were not sensitive to atmospheric CO₂, but were very sensitive to temperature. Prefruiting branch nodal positions required longer to develop than nodes with fruiting branches. Carbon dioxide levels did not affect the time required to produce nodes. Number of branches produced was sensitive to both temperature and CO₂. The larger number of bells set on the lower branches of plants grown at high CO₂ provided a larger sink for photosynthate than plants grown at low CO₂. This may be the reason for the observed reduction in number of fruit at the upper nodes of high-CO₂-grown plants. More bells and squares were produced and retained on plants grown in high-CO₂ environments, except that none were produced in either CO₂ environment at 40/32 degrees C. Our results indicate that high-temperature-tolerant cotton cultivars would be more productive in the present-day CO₂ world, and they would be essential in the future if global temperature increases.

KEYWORDS: ELEVATED CO₂, ENRICHMENT, GROWTH, PLANTS, RESPONSES

1942

Reddy, K.R., H.F. Hodges, and J.M. McKinion. 1995. Carbon-dioxide and temperature effects on pima cotton growth. *Agriculture Ecosystems & Environment* 54(1-2):17-29.

Temperature and CO₂ are major environmental variables that affect plant growth and development. Limited information is available concerning how these factors affect plants, as well as specific interactions between the two. We conducted two experiments in controlled environmental chambers where temperature and CO₂ were controlled and other environmental factors were not limiting. The purpose was to determine how cotton grew and responded to a range of temperatures and CO₂ concentrations. During vegetative development,

stem growth was quite sensitive to CO₂ resulting in more effective early-season light capture. Plants did not develop more nodes when exposed to additional CO₂, while node number increased more at higher temperatures. Individual leaf growth was about 18% greater at optimum temperature in 450 mul 1(-1) than in 350 mul 1(-1) CO₂, but did not increase from 450 mul 1(-1) CO₂ to 700 mul 1(-1) CO₂. However, the time required for a leaf to reach mature size was not influenced by CO₂. Leaf area, on the whole plant basis, was about 33% greater on plants grown at optimum temperature in high CO₂ than in ambient CO₂. The greater leaf area on a whole plant basis was achieved by a combination of larger leaves and additional leaves produced primarily on the branches. There was a 28% increase in number of bolls produced at 700 mul 1(-1) CO₂ at optimum temperature compared with bolls produced at 350 mul 1(-1) CO₂. There was not, however, an increase in boll size due to high CO₂. At 35.5-degrees-C, little growth response to high CO₂ environments occurred at 700 mul 1(-1) CO₂ compared with 350 mul 1(-1) CO₂, but approximately a 45% increase occurred in the plants grown at 18.9-26.9-degrees-C. Less total biomass was produced at 35.5-degrees-C than at 26.9-degrees-C and no bolls were produced in either CO₂ environment at the higher temperature. The most important response to temperature and CO₂ occurred at high temperatures where the effects of elevated CO₂ on plant growth were masked by apparent high-temperature injury that limited growth of all plant organs, particularly, reproductive growth.

KEYWORDS: ELEVATED CO₂, RESPONSES, RETENTION

1943

Reddy, K.R., H.F. Hodges, and J.M. McKinion. 1997. A comparison of scenarios for the effect of global climate change on cotton growth and yield. *Australian Journal of Plant Physiology* 24(6):707-713.

If global surface temperatures change as projected because of radiative and physiological effects of a changing environment, we should expect important changes in crop production in the 21st Century. Experiments were conducted at ambient and twice ambient atmospheric CO₂ concentrations at five temperatures. The 1995 temperature in Mississippi was used as a reference with the other temperatures being 1995 minus 2 degrees C, and 1995 plus 2, 5 and 7 degrees C. Daily and seasonal variation and amplitudes were maintained. Seedlings had 4-6 times as much leaf area and dry weight at 20 d after emergence when grown at 28 degrees C as at 23 degrees C (1995 ambient) average temperature during that growth period. Number of days to first square, flower, and open boll decreased as temperature increased. Double atmospheric CO₂ did not affect these developmental rates. Temperatures above 28 degrees C, or 1995 average whole-season temperatures, were detrimental to mid- and late-season boll retention and growth. No fruits were retained to maturity at 1995 plus 5 or 7 degrees C. However, whole season vegetative growth was not significantly reduced by temperature 5-7 degrees C above the 1995 ambient conditions. Twice ambient CO₂ caused about 40% increase in vegetative dry matter accumulation across temperatures. In a separate experiment, similar results were obtained on fruiting cotton grown at a range of temperatures based on long-term average US Midsouth July temperatures. Therefore, if global warming occurs as predicted, food and fibre production in such high- temperature and humid environments may be more limited to vegetative structures and the animals that consume vegetative structures.

KEYWORDS: ATMOSPHERIC CO₂, CARBON-DIOXIDE ENRICHMENT, PIMA COTTON, RESPONSES, RICE

1944

Reddy, K.R., H.F. Hodges, and J.M. McKinion. 1997. Modeling temperature effects on cotton internode and leaf growth. *Crop Science* 37(2):503-509.

Cotton (*Gossypium hirsutum* L.) is grown commercially in temperatures that vary greatly during the season. The purpose of this study was to develop potential growth and developmental rates of cotton leaves and internodes as a function of temperature in a temperature-limiting environment. That information may be used with growth duration and appropriate stress factors to develop a crop canopy development model. Plants were grown in sunlit plant growth chambers in five temperatures, 20/12 degrees C to 40/32 degrees C (day/night), at ambient (350 μ mol L⁻¹ CO₂) and twice ambient carbon dioxide levels in well-watered and fertilized conditions. Plants were monitored daily for leaf unfolding dates, areas of leaves, and lengths of internodes at leaf unfolding, and growth of leaves and internodes. Durations of leaf and internode expansion were also determined. Leaf unfolding interval rates of both mainstem and fruiting branches increased as temperature increased; the rate of mainstem leaf unfolding interval increased more than the rate of branch leaf unfolding. Irrespective of sizes, leaves, and internodes fit a single relationship of relative expansion rates and age for each temperature condition. Enriching CO₂ to twice the ambient level did not change these relationships. Increasing temperature increased maximum growth rate, decreased the decay in the rate of expansion due to age, and reduced growth duration of both leaves and internodes. Internodes typically took less time than leaves to elongate at all temperatures. Leaf area and internode length at leaf unfolding increased as temperature increased to 27 to 30 degrees C, then decreased at higher temperatures.

KEYWORDS: CARBON DIOXIDE, GOSSYPIMUM HIRSUTUM L, INITIATION, LEAVES, YIELD

1945

Reddy, K.R., R.R. Robana, H.F. Hodges, X.J. Liu, and J.M. McKinion. 1998. Interactions of CO₂ enrichment and temperature on cotton growth and leaf characteristics. *Environmental and Experimental Botany* 39(2):117-129.

Studies on the interactive effects of atmospheric CO₂ and temperature on growth and leaf morphology, particularly on stomatal index and density are limited. Upland cotton was grown in naturally-lit plant growth chambers at 30/22 degrees C day/night temperatures from planting until squaring or the fifth or sixth leaf emerged. Five growth chambers were maintained at ambient (350 μ mol L⁻¹) CO₂ and another five at twice ambient (700 μ mol L⁻¹) CO₂ throughout the experiment. Day/night temperature treatments of 20/12, 25/17, 30/22, 35/27 and 40/32 degrees C were imposed at each CO₂ treatment for 42 days after squaring. The plants were irrigated with half-strength Hoagland's nutrient solution three times per day. Growth of plant parts was determined at the end of the experiment. Stomatal characteristics, nonstructural carbohydrates and specific leaf weight were measured on the fully expanded tenth mainstem leaf. Stomatal density and index were not affected by elevated CO₂. Stomata and epidermal cell numbers per leaf increased in high CO₂ and were positively correlated with final leaf sizes irrespective of CO₂ level. Our results suggest that plants do not acclimate to elevated CO₂ by changing stomatal density within a single generation. Leaves had greater area and accumulated more biomass when grown in high CO₂. Growth stimulation expressed as dry weight at 700 μ mol L⁻¹ over dry weight at 350 μ mol L⁻¹ CO₂ was uniform across temperatures. Temperature optimum for vegetative and reproductive growth was 30/22 degrees C and was not altered by CO₂ enrichment. Fruit retention was severely curtailed at the two higher temperatures compared to 30/22 degrees C in both CO₂ environments. Increased carbohydrate storage in leaves may be an added advantage for initiation and growth of vegetative structures such as branches at all temperatures. However, it is unlikely that high temperature effects on flower abortion will be ameliorated by high CO₂. Species/cultivars that retain fruits at high temperatures would be more productive both in the present-day cotton producing environments and are even more desirable in the future warmer world. (C) 1998 Elsevier Science B.V. All rights reserved.

KEYWORDS: ATMOSPHERIC CO₂, CARBON DIOXIDE, CLIMATE SENSITIVITY, ELEVATED CO₂, INCREASES, LEAVES, PIMA COTTON, PLANTS, RESPONSES, STOMATAL DENSITY

1946

Reddy, S.R.C., and C. Price. 1999. Carbon sequestration and conservation of tropical forests under uncertainty. *Journal of Agricultural Economics* 50(1):17-35.

Concern for global warming has focused attention on the role of tropical forests in the reduction of ambient CO₂ levels and mitigation of climate change. Deforestation is a major land use change in the tropics, with forest resources undergoing degradation through the influence of logging and conversion to other uses. Land use change is a product of varied local and regional resource use policies. Management of forest resources is one such major temporal factor, influencing resource stability and the carbon pool. Under a given management policy, both the long period of forest growth, and the slow turnover and decay of the carbon pool, enhance the relevance of stand level management policies as cost-effective mechanisms mitigating climate change. Apart from regional level uncertainties like the nature of land use and the estimation of carbon storage in vegetation and soil, the carbon flux of tropical forests is greatly influenced by uncertainty in regenerative capacity of forests and in harvest and management policies. A case study from India is used to develop a transition matrix model of natural forest management, and to explore the economic implications of maintaining and expanding existing carbon sinks. The study further explores the significance of investments in additional carbon sink in plantation forests, given continued uncertainty in natural forest management.

KEYWORDS: BIOMASS, CLIMATE, DAMAGE, LAND, MANAGEMENT, SOUTHEAST-ASIA, STORAGE, TRANSITION

1947

Reddy, V.R., K.R. Reddy, and B. Acock. 1995. Carbon-dioxide and temperature interactions on stem extension, node initiation, and fruiting in cotton. *Agriculture Ecosystems & Environment* 55(1):17-28.

Understanding the response of agricultural crops to rising carbon dioxide concentration (CO₂) and temperature is critical for modeling the effects of future climate change on crop productivity. The objective of this study was to evaluate the direct and interactive effects of temperature and CO₂ on mainstem and branch expansion rates, node initiation rates, and fruiting in cotton to be used for the development of a cotton simulation model. Cotton plants (*Gossypium hirsutum* L., cv. DPL 50) were grown in plant growth chambers exposed to natural light levels with temperature and CO₂ as treatments. The average temperatures were 17.8, 18.7, 22.7, 26.6, and 30.6 degrees C during a 70 day experimental period with CO₂ treatments of 350 and 700 μ mol L⁻¹ at each temperature. Plant height and number of mainstem nodes increased with increase in temperature and CO₂. A nine-fold increase was observed in number of fruiting branches with increase in temperature from 17.8 to 30.6 degrees C, however, no significant differences were observed in fruiting branch number due to doubling of CO₂ except at 30.6 degrees C. The number of days from emergence to first square was strongly influenced by temperature, and CO₂ had no effect on this process. The number of squares and bolls were increased at higher temperatures, and the rate of increase was greater at 700 μ mol L⁻¹ CO₂.

KEYWORDS: AIR- TEMPERATURE, ATMOSPHERIC CO₂ ENRICHMENT, GROWTH, PHOTOSYNTHESIS, SOYBEAN CANOPIES, TRANSPIRATION RESPONSES, YIELD

1948

Reddy, V.R., K.R. Reddy, and H.F. Hodges. 1995. Carbon-dioxide

enrichment and temperature effects on cotton canopy photosynthesis, transpiration, and water-use efficiency. *Field Crops Research* 41(1):13-23.

The objectives of this study were to evaluate effects of ambient and double ambient [CO₂] at a range of growing temperatures on photosynthesis, respiration, transpiration, water-use efficiency and dry matter accumulation of cotton plants (*Gossypium hirsutum* L., cv. DPL 50). In Experiment I, plants were grown outdoors until first bloom, then transferred into naturally lit growth chambers and grown for 22 days at 30/ 18 degrees C with five CO₂ concentrations varying from 350 to 900 μ mol(-1). In Experiment II, air temperatures were maintained at 20/12, 25/17, 30/22, and 35/27 degrees C day/night during a 70-day experimental period with [CO₂] of 350 and 700 μ mol(-1) at each temperature. Photosynthesis increased with [CO₂] from 350 to 700 μ mol(-1) and with temperature. Plants grown at 35/27 degrees C produced fewer bolls due to abscission compared with plants grown at optimum temperatures (30/20 degrees C). At higher [CO₂], water-use efficiency increased at all temperatures due mainly to increased canopy photosynthesis but also to more limited extent to reduced canopy transpiration. Increased photosynthesis at higher [CO₂] resulted in greater dry matter accumulation at all temperatures except at 20/12 degrees C. Respiration increased as dry matter and temperature increased. Plants grown at higher [CO₂] had less respiration per unit dry matter but more per unit area. These results indicate that future increases in [CO₂] are likely to benefit cotton production by increasing carbon assimilation under temperatures favorable for cotton growth. Reduced fruit weights at higher temperatures indicate potential negative effects on production if air temperatures increase as projected in a high-CO₂ world.

KEYWORDS: CLIMATE, CO₂, CROP YIELD, GROWTH, LEAVES, RESPIRATION, RESPONSES, SIMULATION

1949

Reddy, V.R., K.R. Reddy, and Z. Wang. 1997. Cotton responses to nitrogen, carbon dioxide, and temperature interactions (Reprinted from Plant nutrition for sustainable food production and environment, 1997). *Soil Science and Plant Nutrition* 43:1125-1130.

Several studies were conducted to evaluate how increases in the global atmospheric carbon dioxide concentration [CO₂] and temperature affect growth and development rates, dry matter production, photosynthesis, and water use efficiency of cotton and how these responses are influenced by leaf N levels. In one study, cotton (cv. DPL 50) plants were grown at four temperatures (20/12, 25/17, 30/22, and 35/27 degrees C day/night) until harvest at 70 days after emergence (DAE). Each temperature treatment was combined with [CO₂] of 350 or 700 μ mol L⁻¹. In another study, cotton (cv. DES 119) grown at two [CO₂] received five N treatments (0, 1, 2, 6, and 10 mM NO₃ in Hoagland's nutrient solution) at 17 DAE and every 2 days thereafter. Canopy gross photosynthetic rates increased with increasing [CO₂] and temperature. The increased photosynthesis resulted in higher plant growth and dry matter accumulation rates except at the highest temperature. At 70 DAE, the maximum canopy dry matter accumulation rate occurred in 30/22 degrees C. The 35/27 degrees C treatment induced fruit abortion, resulting in greater dry matter accumulation in vegetative structures. Increases in plant dry weights by CO₂ enrichment were greater in the two high temperature regimes than in the two lower temperature regimes. Water-use efficiency increased with increased [CO₂] and decreased with increased temperature. Increases in water-use efficiency were due mainly to increased photosynthesis and partly to reduced canopy transpiration. Increase in leaf N concentration increased cotton photosynthesis and vegetative growth rates, and the increases were higher at 700 μ mol L⁻¹ than at 350 μ mol L⁻¹ [CO₂].

KEYWORDS: CANOPY PHOTOSYNTHESIS, CROP YIELD,

DEFICIENCY, ENRICHMENT, TRANSPIRATION, USE EFFICIENCY, WATER RELATIONS

1950

Reece, C.F., S.V. Krupa, H.J. Jager, S.W. Roberts, S.J. Hastings, and W.C. Oechel. 1995. Evaluating the effects of elevated levels of atmospheric trace gases on herbs and shrubs - a prototype dual array field exposure system. *Environmental Pollution* 90(1):25-31.

In the context of global climate change, an understanding of the long-term effects of increasing concentrations of atmospheric trace gases (carbon dioxide, CO₂, ozone, O₃, oxides of nitrogen, NO_x etc.) on both cultivated and native vegetation is of utmost importance. Over the years, under field conditions, various trace gas-vegetation exposure methodologies with differing advantages and disadvantages have been used. Because of these variable criteria, with elevated O₃ or CO₂ levels, at the present time the approach of free-air experimental-release of the gas into study plots is attracting much attention. However, in the case of CO₂, this approach (using 15 m diameter study plot with a single circular array of vent pipes) has proven to be cost prohibitive (about \$59000- 98000/year/replicate) due to the consumption of significant quantities of the gas to perform the experiment (CO₂ level elevated to 400 ppm above the ambient). Therefore, in this paper, we present a new approach consisting of a dual concentric exposure array of vertical risers or vent pipes. The purpose of the outer array (17 m diameter) is to vent ambient air outward and toward the incoming wind thus providing an air curtain to reduce the velocity of that incoming wind to simulate the mode or the most frequently occurring wind speed at the study site. The inner array (15 m diameter) vents the required elevated levels of trace gases (CO₂, O₃, etc.) into the study plot. This dual array system is designed to provide spatial homogeneity (shown through diffusion modeling) of the desired trace-gas levels within the study plot and to also reduce its consumption. As an example, while in the single- array free-air CO₂-release system the consumption of CO₂ to elevate its ambient concentration by 400 ppm is calculated to be about 980 tons/year/replicate, it is estimated that in the dual array system it would be approximately 590 tons/year/replicate. Thus, the dual array system may provide substantial cost savings (\$24000-39000/year/replicate) in the CO₂ consumption (\$60-100/ton of CO₂) alone. Similarly, benefits in the requirements of other trace gases (O₃, NO_x, etc.) are expected, in future multivariate studies on global climate change.

KEYWORDS: AIR, ENRICHMENT

1951

Reekie, E.G., and F.A. Bazzaz. 1991. Phenology and growth in 4 annual species grown in ambient and elevated CO₂. *Canadian Journal of Botany-Revue Canadienne De Botanique* 69(11):2475-2481.

The objectives of this study were (i) to test the hypothesis that changes in phenology with CO₂ are a function of the effect of CO₂ upon growth and (ii) to determine if CO₂-induced changes in phenology can influence competitive outcome. We examined the effect of 350, 525, and 700- μ mol L⁻¹ CO₂ on *Guara brachycarpa*, *Gailardia pulchella*, *Oenothera lacinata*, and *Lupinus texensis*. Plants were grown as individuals in 150-, 500-, or 1000-mL pots and in competition in 1000-mL pots. Growth and development were monitored at twice-weekly intervals, by recording the number of leaves and noting the presence or absence of stem elongation, branching, flower buds, and open flowers. Elevated CO₂ affected both growth and phenology, but the direction and magnitude of effects varied with species and soil volume. Elevated CO₂ did not appear to affect development through its effect on growth. Those treatments in which there were significant effects of CO₂ on growth were generally different from those treatments in which CO₂ affected phenology. Rather than affecting phenology by changing plant size, CO₂ appeared to affect phenology by modifying the size at which plants

switched from one stage to the next. The level of CO₂ changed competitive outcome; the importance of *Lupinus* increased whereas that of *Oenothera* decreased with increased CO₂. These changes were more closely related to the effect of CO₂ on growth than its effect on phenology.

KEYWORDS: CARBON DIOXIDE, FATE, PHARBITIS, PREDICTIONS, ROSETTE SIZE

1952

Reekie, E.G., C. MacDougall, I. Wong, and P.R. Hicklenton. 1998. Effect of sink size on growth response to elevated atmospheric CO₂ within the genus *Brassica*. *Canadian Journal of Botany-Revue Canadienne De Botanique* 76(5):829-835.

Many plants grown at elevated CO₂ concentrations exhibit enhanced photosynthetic rates. However, this increase in photosynthesis is often reduced after prolonged exposure to elevated CO₂. This reduction may be related to the capacity of plants to utilize the extra photosynthate produced at elevated CO₂. This study examined the effect of source to sink ratio on the capacity of plants to respond to elevated CO₂. Seven species or cultivars within the genus *Brassica* were germinated and grown at either 350 or 1000 ppm CO₂. Broccoli (*Brassica oleracea* L.) and cauliflower (*B. oleracea* L.) have large carbon sinks in the reproductive structures; Chinese broccoli (*Brassica campestris* L.) and marrow stem kale (*B. oleracea*) have carbon sinks in the stem; turnip (*B. campestris*) stores carbon in the root; rape (*Brassica napus* L.) and white mustard (*Brassica alba* (L.) Rabenh.) have no obvious carbon storage structures and were assumed to have a lower sink strength relative to the above cultivars. Plants were harvested at three stages of development and total plant weight, leaf area ratio, and allocation to leaf, root, and stem determined. As young seedlings, all cultivars responded positively to elevated CO₂. The long-term growth response of different cultivars to CO₂ was independent of sink location, but was dependent on sink size. Cultivars with no obvious carbon storage structures showed no significant growth enhancement by elevated CO₂ by the end of the experiment. However, neither leaf area ratio nor biomass allocation pattern were reliable predictors of response to CO₂ suggesting that assessing differences in source to sink ratio is not necessarily straightforward.

KEYWORDS: ENRICHMENT, PHOTOSYNTHESIS, PINE, PLANTS, TEMPERATURE

1953

Reekie, J.Y.C., P.R. Hicklenton, and E.G. Reekie. 1994. Effects of elevated CO₂ on time of flowering in 4 short-day and 4 long-day species. *Canadian Journal of Botany-Revue Canadienne De Botanique* 72(4):533-538.

This study was undertaken to determine if the effect of elevated CO₂ on flowering phenology is a function of the photoperiodic response of the species involved. Four long-day plants, *Achillea millefolium*, *Callistephus chinensis*, *Campanula isophylla*, and *Trachelium caeruleum*, and four short-day plants, *Dendranthema grandiflora*, *Kalanchoe blossfeldiana*, *Pharbitis nil*, and *Xanthium pensylvanicum*, were grown under inductive photoperiods (9 h for short day and 17 h for long day) at either 350 or 1000 $\mu\text{L/L}$ CO₂. Time of visible flower bud formation, flower opening, and final plant biomass were assessed. Elevated CO₂ advanced flower opening in all four long-day species and delayed flowering in all four short-day species. In the long-day species, the effect of CO₂ was primarily on bud initiation; all four species formed buds earlier at high CO₂. Bud development, the difference in time between flower opening and bud initiation, was advanced in only one long-day species, *Callistephus chinensis*. Mixed results were obtained for the short-day species. Elevated CO₂ exerted no effects on

bud initiation but delayed bud development in *Dendranthema* and *Kalanchoe*. In *Xanthium*, bud initiation rather than bud development was delayed. Data on bud initiation and development were not obtained for *Pharbitis*. The negative effect of CO₂ upon phenology in the short-day species was not associated with negative effects on growth. Elevated CO₂ increased plant size in both long-day and short-day species.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, GROWTH, PHARBITIS

1954

Reekie, J.Y.C., P.R. Hicklenton, and E.G. Reekie. 1997. The interactive effects of carbon dioxide enrichment and daylength on growth and development in *Petunia hybrida*. *Annals of Botany* 80(1):57-64.

Plants were grown at either 350 or 1000 $\mu\text{L/L}$ CO₂ and in one of three photoperiod treatments: continuous short days (SD), continuous long days (LD), or short switched to long days at day 41 (SD-LD). All plants received 9 h of light at 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and LD plants received an additional 4 h of light at 8 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Growth of SD plants responded more positively to elevated CO₂ than did LD plants, due largely to differences in the effect of CO₂ on unit leaf rate. High CO₂ increased height and decreased branching under SD conditions, but had no effect under LD conditions. Elevated CO₂ also increased the number of buds and open flowers, the effect for flower number being greater in short than in long days. The specific leaf area of plants grown at 1000 $\mu\text{L/L}$ CO₂ was reduced regardless of daylength. High CO₂ also decreased leaf and increased reproductive allocation, the magnitude of these effects being greater under SD conditions. Bud formation and flower opening was advanced under high CO₂ conditions in SD plants but bud formation was delayed and there was no effect on flower opening under LD conditions. The effects of CO₂ on plants switched from SD to LD conditions were largely intermediate between the two continuous treatments, but for some parameters, more closely resembled one or the other. The results illustrate that daylength is an important factor controlling response of plants to elevated CO₂. (C) 1997 Annals of Botany Company.

KEYWORDS: AMBIENT, C-3, ELEVATED CO₂, INCREASING CO₂ CONCENTRATION, IRRADIANCE, PHARBITIS, PHOTOSYNTHESIS, PLANT GROWTH, RESPONSES, TEMPERATURE

1955

Reeves, D.W., H.H. Rogers, S.A. Prior, C.W. Wood, and G.B. Runion. 1994. Elevated atmospheric carbon-dioxide effects on sorghum and soybean nutrient status. *Journal of Plant Nutrition* 17(11):1939-1954.

Increasing atmospheric carbon dioxide (CO₂) concentration could have significant implications on technologies for managing plant nutrition to sustain crop productivity in the future. Soybean (*Glycine max* [L.] Merr.) (C₃ species) and grain sorghum (*Sorghum bicolor* [L.] Moench) (C₄ species) were grown in a replicated split-plot design using open-top field chambers under ambient (357 $\mu\text{mol/mol}$) and elevated (705 $\mu\text{mol/mol}$) atmospheric CO₂. At anthesis, leaf disks were taken from upper mature leaves of soybean and from the third leaf below the head of sorghum for analysis of plant nutrients. Leaf greenness was measured with a Minolta SPAD-502 chlorophyll meter. Concentrations of chlorophylls a and b and specific leaf weight were also measured. Above-ground dry matter and seed yield were determined at maturity. Seed yield of sorghum increased 17.5% and soybean seed yield increased 34.7% with elevated CO₂. There were no differences in extractable chlorophyll concentration or chlorophyll meter readings due to CO₂ treatment, but meter readings were reduced 6% when sorghum was grown in chambers as compared in the open. Leaf nitrogen (N)

concentration of soybean decreased from 54.5 to 39.1 g/kg at the higher CO₂ concentration. Neither the chambers nor CO₂ had an effect on concentrations of other plant nutrients in either species. Further work under field conditions is needed to determine if current critical values for tissue N in crops, especially C3 crops, should be adjusted for future increases in atmospheric CO₂ concentration.

KEYWORDS: CHLOROPHYLL METER, CO₂- ENRICHMENT, EXCHANGE-RATES, FIELD, GROWTH, MAIZE, MINERAL NUTRITION, NITROGEN STATUS, RESPONSES, WHEAT

1956

Refouvelet, E., and F. Daguin. 1999. Polymorphic glutamate dehydrogenase in lilac vitroplants as revealed by combined preparative IEF and native PAGE: Effect of ammonium deprivation, darkness and atmospheric CO₂ enrichment upon isomerization. *Physiologia Plantarum* 105(2):199-206.

The activity and polymorphism of glutamate dehydrogenase (GDH) were studied in basal callus of Lilac (*Syringa vulgaris* L.) vitroplants. Native PAGE alone revealed seven bands staggered at regular intervals. Preparative liquid-vein IEF allowed the separation of six to ten GDH fractions with charges ranging between 5.18 and 7.08. Analysis of these GDH fractions in native PAGE indicated that up to seven GDH bands can be detected for each fraction. This suggests the existence of seven isoforms of the enzyme with subunits presenting different isoelectric points. Dark- and ammonium-controlled forms were found to be the more acidic and faster migrating ones in native PAGE. The results support for the first time that atmospheric CO₂ enrichment increases GDH activity dramatically and modifies isomerization of the enzyme.

KEYWORDS: ARABIDOPSIS-THALIANA, HIGHER-PLANTS, LEAF, MITOCHONDRIA, NITROGEN ASSIMILATION, SYNTHETASE, TISSUES

1957

Reich, P.B. 1995. Phenology of tropical forests - patterns, causes, and consequences. *Canadian Journal of Botany-Revue Canadienne De Botanique* 73(2):164-174.

Leaf phenology of tropical forests is distinct from other biomes. Unlike the marked temperature-related periodicity of temperate forests, development tends to be continuous in aseasonal lowland tropical rain forests and becomes more episodic in response to increasing annual drought in tropical dry forests. Hence, in tropical rain forests, foliar development (production, senescence, and longevity) is largely under internal rather than environmental control. In contrast, tropical forests with marked annual dry seasons display associated seasonality of leaf production and shedding. This developmental seasonality can be explained by overlaying the influence of seasonality on trees' internally regulated development and appears to be controlled by acclimative physiological processes and not by sensitivity to photo-, thermo-periodic, or direct environmental cues. Consequences of tropical phenology stem from both the variety of leaf and species ecophysiological types common to a given moisture regime and their relative synchrony of development, and include the following: larger diversity of ecophysiological species types in rain than dry forests; differential rates of herbivory in dry than wet seasons and for synchronous versus asynchronous leaf flushes; ecosystems with greater canopy foliar mass per hectare in rain than dry forests; and several leaf adaptations perhaps unique to tropical forests, such as delayed greening and seasonal leaf phenotypes. Tropical forests may vary in sensitivity to predicted climate change. Phenology of rain forests should change little unless water balance changes markedly, and developmental events in rain forests may be relatively insensitive to moderate changes in CO₂ or temperature. Phenology of dry forests could be more sensitive, and in

opposite directions, to elevated CO₂ and temperatures. Elevated CO₂ might delay the onset of leaf shedding and stimulate longer life span if stand level transpiration is reduced, whereas higher temperatures could lead to more rapid water depletion, longer leafless periods, and more strongly synchronized phenology.

KEYWORDS: COSTA-RICA, DECIDUOUS FOREST, DRY FOREST, HERBIVORY, LEAF LIFE-SPAN, LONGEVITY, LOWLANDS, SEASONAL DROUGHT, TREES, UNDERSTORY COMMUNITY

1958

Reich, P.B., J. Oleksyn, and M.G. Tjoelker. 1996. Needle respiration and nitrogen concentration in Scots Pine populations from a broad latitudinal range: A common garden test with field-grown trees. *Functional Ecology* 10(6):768-776.

1. Models of tree function and forest ecosystem carbon budgets often assume that potential global changes in temperature and/or other factors may alter tissue nitrogen (N) and dark respiration rates (R(d)). However, little is known of patterns of co-variation in tissue N and R(d) among intraspecific populations originating along climatic gradients, and of whether an N-based model of R(d) can link these two variables. To address these issues, we studied N and R(d) in fully expanded needles of 10-year-old trees of 14 Scots Pine (*Pinus sylvestris*) populations of wide-ranging origin (43 degrees to 60 degrees N), grown under common garden conditions. 2. For 11 lowland populations (elevation <200 m) from the contiguous part of the species range (48 degrees to 60 degrees N) grown at a field site in Kornik, western Poland (52 degrees N), there were greater needle %N in populations from increasing latitude of origin or decreasing mean annual temperature (r greater than or equal to 0.93, $P < 0.01$). Similar %N and latitude of origin correlations were observed in another year at this site and in retrospective analyses of published data for different sets of Scots Pine populations grown in common gardens at 48 degrees, 52 degrees C and 62 degrees N latitudes. Needle R(d) rates of the 11 lowland populations growing at Kornik and measured at a common temperature (20 degrees C) were greater, by as much as 50%, for more northerly than southerly populations. Mean R(d) rates were positively correlated to latitude of origin and to mean annual temperature ($P < 0.05$, $r = 0.7$ to 0.8). R(d) and needle %N were positively correlated ($P < 0.01$, $r = 0.75$), with one relationship fitting all data. Across the entire range from 1.15 to 1.55 needle %N, R(d) increased from 4.5 to 6.9 nmol g⁻¹ s⁻¹. 3. Mean needle %N and R(d) values for two montane southern populations (43 degrees and 44 degrees N, elevation greater than or equal to 885 m) growing in the same common garden at Kornik were consistent with the relationships between mean annual temperature, needle %N and R(d) observed for the more northerly populations but did not fit the latitudinal patterns. This suggests that temperature and/or associated climate variables are likely the driving force for observed genetic variation in Scots Pine needle %N and R(d) across latitudinal and altitudinal gradients. 4. Results of these common garden studies support the idea of a general relationship between needle dark respiration and N concentration, and indicate that there is intraspecific genetic variation in physiology that is selected by climate that persists in a common environment, resulting in higher needle %N and respiration in plants originating from colder habitats. Such patterns need to be better understood and quantified, and merit consideration in modelling of current and potential global change effects on plant function and global carbon cycles.

KEYWORDS: AIR-POLLUTION, CLIMATE CHANGE, CO₂ EXCHANGE, DARK RESPIRATION, GRADIENTS, MAINTENANCE RESPIRATION, PHOTOSYNTHESIS, PLANTS, SYLVESTRIS L, TEMPERATURE

1959

Reichenauer, T., H.R. BolharNordenkampf, U. Ehrlich, G. Soja,

W.F. Postl, and F. Halbwachs. 1997. The influence of ambient and elevated ozone concentrations on photosynthesis in *Populus nigra*. *Plant, Cell and Environment* 20(8):1061-1069.

Light-saturated net leaf photosynthesis ($A(\text{sat})$), CO_2 response curves (A/C_i), current photochemical capacity (F_v/F_m) and pigment contents were measured in leaves of *Populus nigra* (Clone T107) which had been exposed to ozone stress in open-top chambers for the entire growth period. Surprisingly, not only elevated ($\text{ao}(+)$, i.e. ambient air + 50 $\text{mm}^3 \text{m}^{-3}$ ozone) but also ambient (aa) ozone concentrations led to a reduction in $A(\text{sat})$ in comparison with leaves exposed to air containing almost no ozone ($\text{cf}(-)$, i.e. charcoal filtered ambient air). The very small change in leaf conductance (g_l) indicated that the decrease in $A(\text{sat})$ was not due to stomatal limitation. This finding was supported by the fact that, a decrease in carboxylation efficiency (CE) correlated with a loss in $A(\text{sat})$. In comparison to cf -leaves, aa leaves showed no change in current photochemical capacity (F_v/F_m) throughout the whole experiment. However, a marked decline in F_v/F_m in $\text{ao}(+)$ leaves was observed at a time when $A(\text{sat})$ and CE were already decreased by about 45% and 60% respectively. As the chlorophyll b content of leaves is known to correlate with the amount of LHC and PSII centres, it was used to normalize fluorescence parameters in relation to PSII centres present. The normalized values for F_m and F_o increased with the dosage of ozone in $\text{ao}(+)$ leaves but not in aa leaves, indicating a change of the pigment content of PSII in the former, but not in the latter. These data led to the conclusion that ozone interacts primarily with components of the Calvin cycle, which results in a decrease in $A(\text{sat})$ with subsequent feedback on the current photochemical capacity of PSII centres.

KEYWORDS: AIR- POLLUTANTS, BISPHOSPHATE CARBOXYLASE OXYGENASE, CHLOROPHYLL FLUORESCENCE, $\Delta F/F_o$, EXPOSURE, LEAVES, NET PHOTOSYNTHESIS, PLANTS, STOMATAL CONDUCTANCE, STRESS

1960

Reicosky, D.C., D.W. Reeves, S.A. Prior, G.B. Runion, H.H. Rogers, and R.L. Raper. 1999. Effects of residue management and controlled traffic on carbon dioxide and water loss. *Soil & Tillage Research* 52(3-4):153-165.

Management of crop residues and soil organic matter is of primary importance in maintaining soil fertility and productivity and in minimizing agricultural impact on the environment. Our objective was to determine the effects of traffic and tillage on short-term carbon dioxide (CO_2) and water (H_2O) fluxes from a representative soil in the southeastern Coastal Plain (USA). The study was conducted on a Norfolk loamy sand (FAO classification, Luxic Ferralsols; USDA classification, fine-loamy siliceous, thermic Typic Kandiudults) cropped to a corn (*Zea mays* L.)- soybean (*Glycine max* (L.) Merr) rotation with a crimson clover (*Trifolium incarnatum* L.) winter cover crop for eight years. Experimental variables were with and without traffic under conventional tillage (CT) (disk harrow twice, chisel plow, field cultivator) and no tillage (NT) arranged in a split-plot design with four replicates. A wide-frame tractive vehicle enabled tillage without wheel traffic. Short-term CO_2 and H_2O fluxes were measured with a large portable chamber. Gas exchange measurements were made on both CT and NT at various times associated with tillage and irrigation events. Tillage-induced COP and H_2O fluxes were larger than corresponding fluxes from untilled soil. Irrigation caused the CO_2 fluxes to increase rapidly from both tillage systems, suggesting that soil gas fluxes were initially limited by lack of water. Tillage-induced CO_2 and H_2O fluxes were consistently higher than under NT. Cumulative CO_2 flux from CT at the end of 80 h was nearly three times larger than from NT while the corresponding H_2O loss was 1.6 times larger. Traffic had no significant effects on the magnitude of CO_2 fluxes, possibly reflecting this soil's natural tendency to reconsolidate. The immediate impact of intensive

surface tillage of sandy soils on gaseous carbon loss was larger than traffic effects and suggests a need to develop new management practices for enhanced soil carbon and water management for these sensitive soils. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: BIOMASS, CORN, NITROGEN, SOIL RESPIRATION, TILLAGE SYSTEM

1961

Reid, C.D., and E.L. Fiscus. 1998. Effects of elevated $[\text{CO}_2]$ and/or ozone on limitations to CO_2 assimilation in soybean (*Glycine max*). *Journal of Experimental Botany* 49(322):885-895.

Soybean (*Glycine max*) was grown in open-top field chambers at ambient (360 $\mu\text{mol mol}^{-1}$) or doubled $[\text{CO}_2]$ either in charcoal-filtered air (20 nmol mol^{-1} $[\text{O}_3]$) or in non-filtered air supplemented to 1.5 x ambient $[\text{O}_3]$ (70 nmol mol^{-1}) to determine the major limitations to assimilation under conditions of elevated $[\text{CO}_2]$ and/or $[\text{O}_3]$. Through plant ontogeny, assimilation versus intercellular CO_2 concentration (A/C_i) responses were measured to assess the limitations to assimilation imposed by the capacity for Rubisco carboxylation, RuBP regeneration, and stomatal diffusion. In the vegetative stages, no significant treatment effects of elevated $[\text{CO}_2]$ and/or $[\text{O}_3]$ were observed on Rubisco carboxylation efficiency (CE), light and CO_2 -saturated assimilation capacity ($A(\text{max})$), and chlorophyll content (Chl). However, for plants grown in elevated $[\text{CO}_2]$, the assimilation rate at growth $[\text{CO}_2]$ (A) was 60% higher than at ambient $[\text{CO}_2]$ up to the seed maturation stage, and the potential rate of assimilation by Rubisco capacity ($A(p)$) was increased. Also in elevated $[\text{CO}_2]$: A was 51% of $A(p)$; the relative stomatal limitation (%Stomata) was 5%; and the relative RuBP regeneration limitation (%RuBP) was 44%. In ambient $[\text{CO}_2]$, O_3 gradually decreased A per unit leaf area, but had little effect on A , and the relative limitations to assimilation where A remained 51% of $A(p)$, %Stomata was 27%, and %RuBP was 22%. During reproduction, CE declined for plants grown in elevated $[\text{CO}_2]$ and/or $[\text{O}_3]$; $A(p)$ was unaffected by elevated $[\text{CO}_2]$, but was reduced by $[\text{O}_3]$ at ambient $[\text{CO}_2]$; A increased to 72% of $A(p)$ in elevated $[\text{CO}_2]$ and/or $[\text{O}_3]$ - fumigated air; the %Stomata increased; and the %RuBP decreased, to become non significant in elevated $[\text{CO}_2]$ from the beginning of seed growth on, and in O_3 -fumigated air at ambient $[\text{CO}_2]$ at the seed maturation stage. The decrease in %RuBP occurred concomitantly with an increase in $A(\text{max})$ and Chl . Significant $[\text{CO}_2] \times [\text{O}_3]$ interactions support the lack of an O_3 effect on assimilation and its limitations at elevated $[\text{CO}_2]$ during seed maturation. These data suggest that elevated $[\text{CO}_2]$ alleviated some of the effects of O_3 on photosynthesis.

KEYWORDS: ATMOSPHERIC CO_2 , CARBON DIOXIDE, GAS-EXCHANGE, LEAF PROTEINS, NET PHOTOSYNTHESIS, OPEN-TOP CHAMBERS, RIBULOSE-1,5-BISPHOSPHATE CARBOXYLASE OXYGENASE, SPRING WHEAT, STOMATAL CONDUCTANCE, TRITICUM-AESTIVUM L

1962

Reid, C.D., E.L. Fiscus, and K.O. Burkey. 1998. Combined effects of chronic ozone and elevated CO_2 on Rubisco activity and leaf components in soybean (*Glycine max*). *Journal of Experimental Botany* 49(329):1999-2011.

Content and activity of Rubisco and concentrations of leaf nitrogen, chlorophyll and total non-structural carbohydrates (TNC) were determined at regular intervals during the 1993 and 1994 growing seasons to understand the effects and interactions of $[\text{O}_3]$ and elevated $[\text{CO}_2]$ on biochemical limitations to photosynthesis during ontogeny. Soybean (*Glycine max* var. Essex) was grown in open-top field chambers in either charcoal-filtered air (CF, 20 nmol mol^{-1}) or non-

filtered air supplemented with 1.5 x ambient [O-3] (c. 80 nmol mol⁻¹) at ambient (AA, 360 μ mol mol⁻¹) or elevated [CO₂] (700 μ mol mol⁻¹). Sampling period significantly affected all the variables examined. Changes included a decrease in the activity and content of Rubisco during seed maturation, and increased nitrogen (N), leaf mass per unit area (LMA) and total non- structural carbohydrates (TNC, including starch and sucrose) through the reproductive phases. Ontogenetic changes were most rapid in O-3-treated plants. At ambient [CO₂], O-3 decreased initial activity (14-64% per unit leaf area and 14-29% per unit Rubisco) and content of Rubisco (9-53%), and N content per unit leaf area. Ozone decreased LMA by 17-28% of plants in CF-AA at the end of the growing season because of a 24-41% decrease in starch and a 59-80% decrease in sucrose. In general, elevated [CO₂] in CF or O-3-fumigated air, reduced the initial activity of Rubisco and activation state while having little effect on Rubisco content, N and chlorophyll content, per unit leaf area. Elevated CO₂ decreased Rubisco activity by 14-34% per unit leaf area and 15-25% per unit Rubisco content of plants in grown CF-AA, and increased LMA by 27-74% of the leaf mass per unit area in CF-AA because of a 23-148% increase in starch. However, the data suggest that, at elevated [CO₂], increases in starch and sucrose are not directly responsible for the deactivation of Rubisco. Also, there was little evidence of an adjustment of Rubisco activity in response to starch and sucrose metabolism. Significant interactions between elevated [CO₂] and [O-3] on all variables examined generally resulted in alleviation or amelioration of the O-3 effects at elevated CO₂. These data provide further support to the idea that elevated atmospheric CO₂ will reduce or prevent damage from pollutant O-3.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, LEAVES, NET PHOTOSYNTHESIS, O-3, PHOTOSYNTHETIC APPARATUS, RIBULOSE-1,5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, TOMATO PLANTS, TRITICUM-AESTIVUM L, WHEAT

1963

Reid, C.D., E.L. Fiscus, and K.O. Burkey. 1999. Effects of chronic ozone and elevated atmospheric CO₂ concentrations on ribulose-1,5-bisphosphate in soybean (*Glycine max*). *Physiologia Plantarum* 106(4):378-385.

Ribulose-1,5-bisphosphate (RuBP) pool size was determined at regular intervals during the growing season to understand the effects of tropospheric ozone concentrations, elevated atmospheric carbon dioxide concentrations and their interactions on the photosynthetic limitation by RuBP regeneration. Soybean (*Glycine max* [L.] Merr. cv. Essex) was grown from seed to maturity in open-top field chambers in charcoal-filtered air (CF) either without (22 nmol O-3 mol⁻¹) or with added O-3 (83 nmol mol⁻¹) at ambient (AA, 369 μ mol CO₂ mol⁻¹) or elevated CO₂ (710 μ mol mol⁻¹). The RuBP pool size generally declined with plant age in all treatments when expressed on a unit leaf area and in all treatments but CF-AA when expressed per unit ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco; EC 4.1.1.39) binding site. Although O-3 in ambient CO₂ generally reduced the RuBP pool per unit leaf area, it did not change the RuBP pool per unit Rubisco binding site. Elevated CO₂, in CF or O-3-fumigated air, generally had no significant effect on RuBP pool size, thus mitigating the negative O-3 effect. The RuBP pools were below 2 mol mol⁻¹ binding site in all treatments for most of the season, indicating limiting RuBP regeneration capacity. These low RuBP pools resulted in increased RuBP regeneration. Fia faster RUBP turnover, but only in CF air and during vegetative and flowering stages at elevated CO₂. Also, the low RuBP pool sizes did not always reflect RuBP consumption rates or the RuBP regeneration limitation relative to potential carboxylation (%RuBP). Rather, %RuBP increased linearly with decrease in the RuBP pool turnover time. These data suggest that amelioration of damage from O-3 by elevated atmospheric CO₂ to the RuBP regeneration may be in response to changes in the Rubisco carboxylation.

KEYWORDS: CARBOXYLASE OXYGENASE ACTIVITY, LEAVES, O-3, PHASEOLUS-VULGARIS L, PHOTOSYNTHESIS, PLANTS, POOL SIZES, RIBULOSE 1,5-BISPHOSPHATE, SPRING WHEAT, STATE GAS-EXCHANGE

1964

Reid, C.D., and B.R. Strain. 1994. Effects of CO₂ enrichment on whole-plant carbon budget of seedlings of *Fagus grandifolia* and *Acer saccharum* in low irradiance. *Oecologia* 98(1):31-39.

Carbon exchange rates (CER) and whole-plant carbon balances of beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*) were compared for seedlings grown under low irradiance to determine the effects of atmospheric CO₂ enrichment on shade-tolerant seedlings of co-dominant species. Under contemporary atmospheric CO₂, photosynthetic rate per unit mass of beech was lower than for sugar maple, and atmospheric CO₂ enrichment enhanced photosynthesis for beech only. Aboveground respiration per unit mass decreased with CO₂ enrichment for both species while root respiration per unit mass decreased for sugar maple only. Under contemporary atmospheric CO₂, beech had lower C uptake per plant than sugar maple, while C losses per plant to nocturnal aboveground and root respiration were similar for both species. Under elevated CO₂, C uptake per plant was similar for both species, indicating a significant relative increase in whole-seedling CER with CO₂ enrichment for beech but not for sugar maple. Total C loss per plant to aboveground respiration was decreased for beech only because increase in sugar maple leaf mass counterbalanced a reduction in respiration rates. Carbon loss to root respiration per plant was not changed by CO₂ enrichment for either species. However, changes in maintenance respiration cost and nitrogen level suggest changes in tissue composition with elevated CO₂. Beech had a greater net daily C gain with CO₂ enrichment than did sugar maple in contrast to a lower one under contemporary CO₂. Elevated CO₂ preferentially enhances the net C balance of beech by increasing photosynthesis and reducing respiration cost. In all cases, the greatest C lost was by roots, indicating the importance of belowground biomass in net C gain. Relative growth rate estimated from biomass accumulation was not affected by CO₂ enrichment for either species possibly because of slow growth under low light. This study indicates the importance of direct effects of CO₂ enrichment when predicting potential change in species distribution with global climate change.

KEYWORDS: ATMOSPHERIC CO₂ CONCENTRATION, CLIMATE CHANGE, ELEVATED CO₂, GAS-EXCHANGE, GROWTH, LIQUIDAMBAR-STYRACIFLUA, PHOTOSYNTHESIS, PINUS-TAEDA SEEDLINGS, RESPIRATION, WATER-STRESS

1965

Reid, C.D., D.T. Tissue, E.L. Fiscus, and B.R. Strain. 1997. Comparison of spectrophotometric and radioisotopic methods for the assay of Rubisco in ozone-treated plants. *Physiologia Plantarum* 101(2):398-404.

Radioisotopic and spectrophotometric assays for ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) initial and final activities and Rubisco content were compared in plants chronically exposed to ozone (O-3) in a greenhouse and the field. In a greenhouse experiment, *Glycine max* was treated in exposure chambers with either charcoal-filtered air (CF air) or 100 nl O-3 l⁻¹ for 6 h daily during vegetative growth. Samples were collected after 7 days of exposure. In a field experiment, *G. max* was treated in open-top chambers with either CF air or nonfiltered air with O-3 added at 1.5 times ambient O-3 for 12 h daily. Average daily O-3 concentrations were 21 and 92 nl l⁻¹ in the CF and O-3 treatments, respectively samples were collected during vegetative and reproductive growth. Both assays generally yielded comparable Rubisco initial and final activities for greenhouse-grown

plants regardless of the O-3 treatment. However for field-grown plants, Rubisco initial and final activities averaged 15 and 23% lower when assayed by the spectrophotometric rather than the radioisotopic method. For Rubisco content estimated by the spectrophotometric method, lower r^2 values for the regression of Rubisco activity vs concentration of carboxyarabinitol-1,5-bisphosphate were observed in O-3- than in CF-treated plants. Both assays yielded comparable Rubisco contents in the greenhouse and in the field although the variation was larger with the spectrophotometric method in field-grown plants. Growth conditions, field vs greenhouse, were more critical to the spectrophotometric assay performance than the O-3 treatments for measurement of Rubisco activity and content.

KEYWORDS: 1,5-BISPHOSPHATE, ACTIVATION, ELEVATED CO₂, LIGHT-DEPENDENT REGULATION, NET PHOTOSYNTHESIS, PHASEOLUS-VULGARIS L, POOL SIZES, RIBULOSE BISPHOSPHATE CARBOXYLASE, RIBULOSE-1,5-BISPHOSPHATE CARBOXYLASE, RUBP CARBOXYLASE

1966

Reinert, R.A., G. Eason, and J. Barton. 1997. Growth and fruiting of tomato as influenced by elevated carbon dioxide and ozone. *New Phytologist* 137(3):411-420.

'Tiny Tim' tomato plants were exposed to five CO₂ treatments (375 (ambient), 450, 525, 600 or 675 $\mu\text{mol mol}^{-1}$) in combination with O-3 (O or 80 nmol mol^{-1}). Biomass was evaluated following 3, 5, 7 and 13 wk exposure. Biomass following 13 wk exposure also included weekly harvests of mature tomato fruit beginning week 8. Carbon dioxide enrichment significantly enhanced total vegetative plant d. wt at each harvest, as well as cumulative yield of mature fruit, whereas O-3 significantly suppressed total Vegetative plant d. wt at each harvest and reduced total cumulative fruit yield. The magnitude of these changes varied with the development of tomato from early growth to mature fruit yield. Carbon dioxide enrichment reduced the detrimental effects of O-3 on total vegetative plant d. wt of tomato following 3, 5, 7 and 13 wk exposure. Final mature fruit yield was 24% higher under enriched CO₂ treatments than in ambient CO₂. Ozone suppressed final yield by 31% following exposure to 80 nmol mol^{-1} O-3 when compared with exposure to charcoal-filtered (CF) air. The impacts of both CO₂ and O-3 on yield were, however, dependent upon the presence or absence of the other gas. In the absence of O-3, yields were very similar for the ambient and elevated CO₂ treatments, but in the presence of O-3, yields under ambient CO₂ were greatly suppressed whereas yields under elevated CO₂ were similar to those in the absence of O-3. Thus, enriched CO₂ ameliorated most of the suppressive effect of O-3 on yield of mature fruit.

KEYWORDS: ATMOSPHERIC CO₂, CO₂- ENRICHMENT, ENVIRONMENT, EXCHANGE, PHOTOSYNTHETIC ACCLIMATION, RADISH, RESPONSES, TEMPERATURE, VEGETATION, YIELD

1967

Reinert, R.A., and M.C. Ho. 1995. Vegetative growth of soybean as affected by elevated carbon- dioxide and ozone. *Environmental Pollution* 89(1):89-96.

The effects of elevated carbon dioxide (CO₂) and ozone (O-3) on soybean (*Glycine max* (L.) Merr. cv. Centennial) growth and biomass partitioning were evaluated under greenhouse conditions. Soybeans were exposed to CO₂ concentrations at 350 (ambient), 450, 550, and 650 $\mu\text{l liter}^{-1}$ (ppm) for 24 h day⁻¹ for 5 weeks. Ozone treatments of 0 and 120 nl liter^{-1} (ppb) for 6 h day⁻¹ for 5 days week⁻¹ for 5 weeks were added in combination with the CO₂ treatments. Plant dry weight and biomass partitioning were assessed each week. Dry weight of leaf, stem, and root, as well as the total plant dry weight increased with exposure to

increasing levels of CO₂. Dry weight of leaf, root and total plant were suppressed significantly by the O-3 treatment. Stem dry weight was not affected by O-3. Suppression of root dry weight due to O-3 at each weekly harvest was significantly dependent on the CO₂ concentration. Root growth was enhanced by CO₂ at 650 $\mu\text{l liter}^{-1}$ compared with ambient CO₂ (350 $\mu\text{l liter}^{-1}$) at 5 weeks of age. At ambient CO₂ in the presence of O3 the roots were only about 63% of the weight of the root grown in the absence of O-3. At 550 and 650 $\mu\text{l liter}^{-1}$ CO₂ the biomass of soybean roots in the presence of 120 nl liter^{-1} O-3 was 88.2 and 88.4% of the control, respectively. Thus, CO₂ limited the amount of root growth suppression caused by O-3. The partitioning of leaf, stems and root dry weight in relation to total plant dry weight remained relatively constant across each CO₂ concentration. Thus, CO₂ did not affect biomass partitioning among leaves, stems and roots of soybean.

KEYWORDS: CO₂- ENRICHMENT, COMBINATION, EXPOSURE, FIELD, NITROGEN, PHOTOSYNTHESIS, RESPONSES, SEED YIELD, SOIL-WATER DEFICIT, TEMPERATURE

1968

Reining, E. 1994. Acclimation of C-3 photosynthesis to elevated co₂ - hypotheses and experimental-evidence. *Photosynthetica* 30(4):519-525.

Acclimation of the photosynthesis of C-3 plants to elevated atmospheric CO₂ concentrations is frequently observed. Some hypotheses frequently proposed to explain this phenomenon are: (1) stomatal closure; (2) inhibition of photosynthesis by starch accumulation, and (3) reduced activity or concentration of ribulose-1,5-bisphosphate carboxylase/oxygenase. These hypotheses are compared with experimental evidence from the literature.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CARBOHYDRATE, ENRICHMENT, GAS-EXCHANGE, GROWTH, LONG-TERM EXPOSURE, PHASEOLUS-VULGARIS L, PLANTS, RIBULOSE BISPHOSPHATE CARBOXYLASE, STARCH

1969

Reining, F. 1995. The effect of elevated co₂ concentrations on the competition between lamium-galeobdolon and stellaria-holostea. *Photosynthetica* 31(4):501-508.

The effect of enhanced air CO₂ concentrations (c(520) and c(650) = 520 and 650 $\text{cm}^3 \text{m}^{-3}$) on the growth of *Lamium galeobdolon* and *Stellaria holostea* and on the competition between the two species was examined. After five months growth under CO₂ enrichment the dry masses of both species increased when the plants were grown in monoculture, but the increase in biomass was much more pronounced in *Stellaria*. When the plants were grown together in competition, the measured shoot masses of *Stellaria* were again higher under c(520) and c(650) than at ambient CO₂ concentration (c(390) = 390 $\text{cm}^3 \text{m}^{-3}$), while the shoot masses of *lamium* strongly decreased at c(650). The effect of CO₂ enrichment on the two plant species in monoculture differed significantly from that observed in mixed cultures. In terms of plant relative yield, *Stellaria* benefitted slightly but insignificantly from competition, while *Lamium* was significantly suppressed under c(650). Total community production of the mixed culture was optimum at c(520), while that of the monocultures was highest at c(650). At c(390) and c(520), growth of *Stellaria* depended strongly on irradiance in all types of culture. At c(650) no such dependence could be demonstrated.

KEYWORDS: ANNUALS, ASSEMBLAGE, CARBON DIOXIDE, CROP RESPONSES, ENRICHMENT, GROWTH, OLD- FIELD PERENNIALS, PLANTS

1970

Reitz, S.R., D.N. Karowe, M.M. Diawara, and J.T. Trumble. 1997. Effects of elevated atmospheric carbon dioxide on the growth and linear furanocoumarin content of celery. *Journal of Agricultural and Food Chemistry* 45(9):3642-3646.

The effects of elevated atmospheric carbon dioxide on the growth and development of celery (*Apium graveolens*) were examined to determine if anticipated global increases in CO₂ will affect the nutritional quality and secondary chemistry of celery. The size (fresh and dry mass), nitrogen and carbon composition, and concentrations of linear furanocoumarins of celery grown under ambient (363 µ L L⁻¹) and elevated (718 µ L L⁻¹) carbon dioxide were analyzed. Growth under elevated CO₂ resulted in larger petioles, reduced nitrogen content, and higher C:N ratios in both leaves and petioles. However, CO₂ treatment did not affect plant water content or carbon content. Moreover, in contrast to the carbon-nutrient balance hypothesis, the increased C:N ratios of plants grown under elevated CO₂ were not associated with increased concentrations of potentially harmful linear furanocoumarins. Levels of linear furanocoumarins in the petioles of plants from each treatment did not exceed concentrations reported to cause acute or chronic contact dermatitis.

KEYWORDS: ALLELOCHEMICALS, ALLOCATION PATTERNS, CO₂ ENVIRONMENTS, ELEMENTAL ORGANIC-ANALYSIS, ENRICHMENT, INTEGRATED PEST-MANAGEMENT, NUTRIENT BALANCE, PERFORMANCE, RESISTANCE, RESPONSES

1971

Rennenberg, H., and A. Gessler. 1999. Consequences of N deposition to forest ecosystems - Recent results and future research needs. *Water, Air, and Soil Pollution* 116(1-2):47-64.

Wet and dry deposition of atmospheric nitrogen (N) compounds into forest ecosystems and their effect on physical, chemical and microbial processes in the soil has attracted considerable attention for many years. Still the consequences of atmospheric N deposition on N metabolism of trees and its interaction with soil microbial processes has only recently been studied. Atmospheric N deposited to the leaves is thought to enter the general N metabolism of the leaves, but the processes involved, the interaction with different metabolic pathways, and the connection between injury by atmospheric N and its metabolic conversion are largely unknown. Laboratory and field experiments have shown that N of atmospheric NO₂ and NH₃, deposited to the leaves of trees, is subject to long-distance transport in the phloem to the roots. This allocation can result in considerable decline of N uptake by the roots. Apparently, the flux of N from the soil into the roots can be down-regulated to an extent that equals N influx into the leaves. This down-regulation is not mediated by generally enhanced amino-N contents, but by elevated levels of particular amino acids. Field experiments confirm these results from laboratory studies: Nitrate (NO₃) uptake by the roots of trees at a field sites exposed to high loads of atmospheric N is negligible, provided concentrations of Gln in the roots are high. At the ecosystem level, consequences of reduced N uptake by the roots of trees exposed to high loads of atmospheric N are (1) an increased availability of N for soil microbial processes, (2) enhanced emission of gaseous N-oxides from the soil, and (3) elevated leaching of NO₃ into the ground water. How recent forest management practices aimed at transforming uniform monocultures to more structured species-rich forests will interact with these processes remains to be seen. Possible implications of these forest management practices on N metabolism in trees and N conversion in the soil are discussed particularly in relation to atmospheric N deposition.

KEYWORDS: AMINO-ACIDS, ATMOSPHERIC AMMONIA, DYNAMIC CHAMBER EXPERIMENTS, ELEVATED CO₂, GLUTAMINE-SYNTHETASE ISOFORMS, HORDEUM VULGARE L., L. KARST, NITRATE REDUCTASE, NITROGEN-DIOXIDE, SPRUCE PICEA-ABIES

1972

Repo, T., H. Hanninen, and S. Kellomaki. 1996. The effects of long-term elevation of air temperature and CO₂ on the frost hardiness of Scots pine. *Plant, Cell and Environment* 19(2):209-216.

The frost hardiness of 20 to 25-year-old Scots pine (*Pinus sylvestris* L.) saplings was followed for 2 years in an experiment that attempted to simulate the predicted climatic conditions of the future, i.e. increased atmospheric CO₂ concentration and/or elevated air temperature. Frost hardiness was determined by an electrolyte leakage method and visual damage scoring on needles. Elevated temperatures caused needles to harden later and dehardening earlier than the controls. In the first year, elevated CO₂ enhanced hardening at elevated temperatures, but this effect disappeared the next year. Dehardening was hastened by elevating CO₂ in both springs. The frost hardiness was high (<-40 degrees C), even at elevated temperatures, in midwinter, at which time the electrolyte leakage method underestimated the frost hardiness compared with the visual scoring. In addition to the significant differences between treatments, there was also significant variation between trees in frost hardiness within treatments. These results suggest that the risks of frost damage are marked in the predicted climatic conditions in Finland, and, more specifically, they depend on how the occurrence of the frost episodes changes with respect to climatic warming during the annual cycle, especially in the autumn and spring. We also conclude that the conditions in midwinter are not critical for frost injury to trees in the future.

KEYWORDS: BUDBURST, DAMAGE, SEASONAL-CHANGES, SEEDLINGS, TREES

1973

Retamales, J., T. Cooper, J. Streif, and J.C. Kania. 1992. Preventing cold-storage disorders in nectarines. *Journal of Horticultural Science* 67(5):619-626.

A storage experiment was aimed at preventing low temperature storage disorders in nectarine fruits, of cvs July Red and Autumn Grand. Fruit was either cooled immediately after harvest or kept at 20-degrees-C for 48 h, before transfer to controlled atmosphere (CA) conditions at 0-degrees-C. Combinations of 0, 10, 15 and 20% CO₂ with 8 and 16% O₂ were assayed. The fruit was evaluated following cold storage, 31 days after harvest, and after four and eight days under 'shelf conditions' (ripening at 15-18-degrees-C). Warming of the fruit at 20-degrees-C before cold storage prevented woolliness in the absence of elevated CO₂ levels but did not affect internal browning and increased reddish discoloration; further, it enhanced water loss and ripening, increasing fruit softening markedly. Conversely, high CO₂ delayed fruit ripening in CA storage, keeping the fruit firmer, and preventing the development of woolliness, internal browning and reddish discoloration during ripening, the best results being mostly obtained with 20% CO₂. O₂ levels assayed did not show clear effects, but decreased O₂ concentration in absence of high CO₂ showed some benefit in 'July Red'. No deleterious effect of CO₂ concentrations even as high as 20% could be detected. Thus, even though high CO₂ in CA conditions showed promise for controlling disorders and preventing over-ripening, further work is needed on other cultivars, and lower O₂ concentrations should be investigated before making a general recommendation.

KEYWORDS: INTERNAL BREAKDOWN, PEACHES, TEMPERATURES

1974

Retuerto, R., L. Rochefort, and F.I. Woodward. 1996. The influence of plant density on the responses of *Sinapis alba* to CO₂ and windspeed. *Oecologia* 108(2):241-251.

Plants in nature live in populations of variable density, a characteristic which may influence individual plant responses to the environment. We investigated how the responses of *Sinapis alba* plants to different wind speeds and CO₂ concentrations could be modified by plant density. In our wind- density experiment the expectation that mechanical and physiological effects of wind will be ameliorated by growing in high density, as a result of positive plant interactions, was realised. Although individual plants were smaller at higher densities, the effect of increasing windspeed was much less than at lower plant densities. A similar reduced sensitivity of individual plant growth under high densities was also observed under CO₂ enrichment. When measured as a population or stand response, there was no effect of density on the CO₂ responses, with all stands showing very similar increases in total biomass with CO₂ enrichment. In the wind speed experiment, total biomass per stand increased significantly with density, although there was no effect of density on the wind speed response. Specific leaf area decreased with increasing wind speed and this response was significantly affected by the density at which the plants grew.

KEYWORDS: BIOMASS ALLOCATION, CANOPY STRUCTURE, CARBON DIOXIDE, GROWTH, LEAF-AREA, LIGHT, PHOTOSYNTHESIS, SIZE, WATER RELATIONS, WIND

1975

Retuerto, R., and F.I. Woodward. 1993. The influences of increased CO₂ and water-supply on growth, biomass allocation and water-use efficiency of *sinapis-alba* L grown under different wind speeds. *Oecologia* 94(3):415-427.

We examined how independent and interactive effects of CO₂ concentrations, water supply and wind speed affect growth rates, biomass partitioning, water use efficiency, diffusive conductance and stomatal density of plants. To test the prediction that wind stress will be ameliorated by increased CO₂ and/or by unrestricted water supply we grew *Sinapis alba* L. plants in controlled chambers under combinations of two levels of CO₂ (350 ppmv, 700 ppmv), two water regimes and two wind speeds (0.3 ms⁻¹, 3.7 ms⁻¹). We harvested at ten different dates over a period of 60 days. A growth analysis was carried out to evaluate treatment effects on plant responses. Plants grown both in increased CO₂ and in low wind conditions had significantly greater stem length, leaf area and dry weights of plant parts. Water supply significantly affected stem diameter, root weight and leaf area. CO₂ enrichment significantly increased the rate of biomass accumulation and the relative ratio of biomass increase to leaf area expansion. High wind speed significantly reduced plant growth rates and the rate of leaf area expansion was reduced more than the rate of biomass accumulation. Regression analysis showed significant CO₂ effects on the proportion of leaf and stem dry weight to total dry weight. A marked plant-age effect was dependent on water supply, wind speed and CO₂ concentration. A reduced water supply significantly decreased the stomatal conductance, and water use efficiency significantly increased with a limited water supply, low wind and increased CO₂. We found significant CO₂ x wind effects for water diffusion resistance, adaxial number of stomata and water use efficiencies and significant wind x water effect for water use efficiency. In conclusion, wind stress was ameliorated by growing in unrestricted water but not by growing in increased CO₂.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, DIFFERENT IRRADIANCE LEVELS, ECOSYSTEMS, ELEVATED CO₂, ENRICHMENT, LEAF-AREA, LIQUIDAMBAR- STYRACIFLUA, PINUS-TAEDA SEEDLINGS, PLANT GROWTH, STOMATAL DENSITY

1976

Reuveni, J., and B. Bugbee. 1997. Very high CO₂ reduces photosynthesis, dark respiration and yield in wheat. *Annals of Botany* 80(4):539-546.

Although terrestrial CO₂ concentrations, [CO₂], are not expected to reach 1000 μmol mol⁻¹ for many decades, CO₂ levels in closed systems such as growth chambers and glasshouses, can easily exceed this concentration. CO₂ levels in life support systems in space can exceed 10 000 μmol mol⁻¹ (1 %). Here we studied the effect of six CO₂ concentrations, from ambient up to 10000 μmol mol⁻¹, on seed yield, growth and gas exchange of two wheat cultivars (USU-Apogee and Veery- 10). Elevating [CO₂] from 350 to 1000 μmol mol⁻¹ increased seed yield (by 33 %), vegetative biomass (by 25 %) and number of heads m⁻² (by 34 %) of wheat plants. Elevation of [CO₂] from 1000 to 10000 μmol mol⁻¹ decreased seed yield (by 37 %), harvest index (by 14%), mass per seed (by 9 %) and number of seeds per head (by 29 %). This very high [CO₂] had a negligible, non-significant effect on vegetative biomass, number of heads m⁻² and seed mass per head. A sharp decrease in seed yield, harvest index and seeds per head occurred by elevating [CO₂] from 1000 to 2600 μmol mol⁻¹. Further elevation of [CO₂] from 2600 to 10000 μmol mol⁻¹ caused a further but smaller decrease. The effect of CO₂ on both wheat cultivars was similar for all growth parameters. Similarly there were no differences in the response to high [CO₂] between wheat grown hydroponically in growth chambers under fluorescent lights and those grown in soilless media in a glasshouse under sunlight and high pressure sodium lamps. There was no correlation between high [CO₂] and ethylene production by flag leaves or by wheat heads. Therefore, the reduction in seed set in wheat plants is not mediated by ethylene. The photosynthetic rate of whole wheat plants was 8 % lower and dark respiration of the wheat heads 25 % lower when exposed to 2600 μmol mol⁻¹ CO₂ compared to ambient [CO₂]. It is concluded that the reduction in the seed set can be mainly explained by the reduction in the dark respiration in wheat heads, when most of the respiration is functional and is needed for seed development. (C) 1997 Annals of Botany Company.

KEYWORDS: CARBON DIOXIDE, ENHANCEMENT, ENRICHMENT, ETHYLENE PRODUCTION, GROWTH, INTACT SUNFLOWER PLANTS, LEAVES, LIGHT, PHYSIOLOGY, RELEASE

1977

Reuveni, J., J. Gale, and A.M. Mayer. 1993. Reduction of respiration by high ambient CO₂ and the resulting error in measurements of respiration made with O₂ electrodes. *Annals of Botany* 72(2):129-131.

KEYWORDS: EFFLUX, ELEVATED CARBON-DIOXIDE, ENRICHMENT, GROWTH, LEAVES, PHOTOSYNTHESIS

1978

Reuveni, J., J. Gale, and M. Zeroni. 1997. Differentiating day from night effects of high ambient [CO₂] on the gas exchange and growth of *Xanthium strumarium* L exposed to salinity stress. *Annals of Botany* 79(2):191-196.

Sodium chloride, at a concentration of 88 mol m⁻³ in half strength Hoagland nutrient solution, increased dry weight per unit area of *Xanthium strumarium* L. leaves by 19%, and chlorophyll by 45% compared to plants grown without added NaCl at ambient (350 μmol mol⁻¹) CO₂ concentration. Photosynthesis, per unit leaf area, was almost unaffected. Even so, over a 4-week period, growth (dry weight increment) was reduced in the salt treatment by 50%. This could be ascribed to a large reduction in leaf area (>60%) and to an approx. 20% increase in the rate of dark respiration (R_d). Raising ambient [CO₂] from zero to 2000 μmol mol⁻¹ decreased R_d in both control and salinized plants (by 20% at 1000, and by 50% at 2000 μmol mol⁻¹ CO₂ concentration) compared to R_d in the absence of ambient CO₂. High night-time [CO₂] had no significant effect on growth of non-salinized plants, irrespective of day-time ambient [CO₂]. Growth reduction caused by salt was reduced from 51% in plants grown in 350 μmol mol⁻¹ throughout the day, to 31% in those grown continuously

in 900 $\mu\text{mol mol}^{-1}$ $[\text{CO}_2]$. The effect of $[\text{CO}_2]$ at night on salinized plants depended on the daytime CO_2 concentration. Under 350 $\mu\text{mol mol}^{-1}$ day-time $[\text{CO}_2]$, 900 $\mu\text{mol mol}^{-1}$ at night reduced growth over a 4-week period by 9% ($P < 0.05$) and 1700 $\mu\text{mol mol}^{-1}$ reduced it by 14% ($P < 0.01$). However, under 900 $\mu\text{mol mol}^{-1}$ day-time $[\text{CO}_2]$, 900 vs. 350 $\mu\text{mol mol}^{-1}$ $[\text{CO}_2]$ at night increased growth by 17% ($P < 0.01$). It is concluded that there is both a functional and an otiose (functionless) component to R_d , which is increased by salt. Under conditions of low photosynthesis (such as here, in the low day-time $[\text{CO}_2]$ regime) the otiose component is small and high night-time $[\text{CO}_2]$ partly suppresses functional R_d , thereby reducing salt tolerance. In plants growing under conditions which stimulate photosynthesis (e.g. with increased daytime $[\text{CO}_2]$), elevated $[\text{CO}_2]$ at night suppresses mainly the otiose component of respiration, thus increasing growth. Consequently, in regions of adequate water and sunlight, the predicted further elevation of the world atmospheric $[\text{CO}_2]$ may increase plant salinity tolerance. (C) 1997 Annals of Botany Company.

KEYWORDS: DARK RESPIRATION RATE, ELEVATED CARBON-DIOXIDE, ENRICHMENT, *LOLIUM-PERENNE*, MAINTENANCE RESPIRATION, MATURE LEAVES, PHOTOSYNTHESIS, PLANTS, SELECTION, TEMPERATURE

1979

Reuveni, J., A.M. Mayer, and J. Gale. 1995. High ambient carbon-dioxide does not affect respiration by suppressing the alternative, cyanide-resistant pathway. *Annals of Botany* 76(3):291-295.

Total dark respiration ($v(t)$), cytochrome pathway ($v(\text{eyt})$), alternative pathway ($v(\text{alt})$) and residual ($v(\text{res})$) respiration were measured in *Lemna gibba* plants, by the use of pathway inhibitors. NaCN was used to inhibit $v(\text{eyt})$ and SHAM (salicylhydroxamic acid) to inhibit $v(\text{alt})$. Residual respiration ($v(\text{res})$) was about 5% of $v(t)$. The effect of high (100 Pa) and low (0 Pa) carbon dioxide partial pressure ($[\text{CO}_2]$) on $v(t)$, $v(\text{eyt})$ and $v(\text{alt})$ was determined from both CO_2 efflux and O_2 uptake measurements. The higher $[\text{CO}_2]$ suppressed $v(t)$ by about 30%. When respiration operated through the cytochrome pathway only, in the absence of $v(\text{alt})$, it was suppressed by about 12% as measured by the O_2 uptake of submerged *Lemna* fronds or by about 40% as measured by CO_2 efflux from Boating fronds. The higher $[\text{CO}_2]$ treatment had only a small effect on respiration, when $v(\text{alt})$ alone operated. There was no evidence of a specific suppression of the $v(\text{alt})$ pathway by high $[\text{CO}_2]$. Succinic dehydrogenase activity of the mitochondria of roots of *Medicago sativum* was reduced by 18%, when the mitochondria were pre-treated with 120 as compared to 34 Pa $[\text{CO}_2]$. There was no such effect on cytochrome c oxidase activity of mitochondria under the same conditions. It is concluded that there is no evidence for the hypothesis that the high $[\text{CO}_2]$ suppression of respiration is a result of a CO_2 effect on the non-phosphorylating alternative respiration pathway. (C) 1995 Annals of Botany Company

KEYWORDS: DARK RESPIRATION, ELEVATED CO_2 , ENRICHMENT, GROWTH, INHIBITION, LEAVES, MITOCHONDRIA, OXIDASE, PLANT RESPIRATION, TEMPERATURE

1980

Rey, A., and P.G. Jarvis. 1997. Growth response of young birch trees (*Betula pendula* Roth.) after four and a half years of CO_2 exposure. *Annals of Botany* 80(6):809-816.

A field experiment consisting of 18 birch trees grown in open top chambers in ambient and elevated CO_2 concentrations was set up with the aim of testing whether the positive growth response observed in many short-term studies is maintained after several growing seasons. We present the results of growth and biomass after 4.5 years of CO_2 exposure, one of the longest studies so far on deciduous tree species. We

found that elevated CO_2 led to a 58% increase in biomass at the end of the experiment. However, estimation of stem mass during the growing season showed that elevated CO_2 did not affect relative growth rate during the fourth growing season, and therefore, that the large accumulation of biomass was the result of an early effect on relative growth rate in previous years. Trees grown in elevated CO_2 invested more carbon into fine roots and had relatively less leaf area than trees grown in ambient CO_2 . In contrast with previous studies, acceleration of growth did not involve a significant decline in nutrient concentrations of any plant tissue. It is likely that increased fine root density assisted the trees in meeting their nutrient demands. Changes in the species composition of the ectomycorrhizal fungi associated with the trees grown in elevated CO_2 in favour of late successional species supports the hypothesis of an acceleration of the ontogeny of the trees in elevated CO_2 . (C) 1997 Annals of Botany Company.

KEYWORDS: CARBON DIOXIDE, ELEVATED ATMOSPHERIC CO_2 , ENRICHMENT, GAS-EXCHANGE, LEAF ANATOMY, MINERAL NUTRITION, NUTRIENT STATUS, POPLAR CLONES, SEEDLINGS, SOUR ORANGE TREES

1981

Rey, A., and P.G. Jarvis. 1998. Long-term photosynthetic acclimation to increased atmospheric CO_2 concentration in young birch (*Betula pendula*) trees. *Tree Physiology* 18(7):441-450.

To study the long-term response of photosynthesis to elevated atmospheric CO_2 concentration in silver birch (*Betula pendula* Roth.), 18 trees were grown in the field in open-top chambers supplied with 350 or 700 $\mu\text{mol mol}^{-1}$ CO_2 for four consecutive growing seasons. Maximum photosynthetic rates, stomatal conductance and CO_2 response curves were measured over the fourth growing season with a portable photosynthesis system. The photosynthesis model developed by Farquhar et al. (1980) was fitted to the CO_2 response curves. Chlorophyll, soluble proteins, total nonstructural carbohydrates, nitrogen and Rubisco activity were determined monthly. Elevated CO_2 concentration stimulated photosynthesis by 33% on average over the fourth growing season. However, comparison of maximum photosynthetic rates at the same CO_2 concentration (350 or 700 $\mu\text{mol mol}^{-1}$) revealed that the photosynthetic capacity of trees grown in an elevated CO_2 concentration was reduced. Analysis of the response curves showed that acclimation to elevated CO_2 concentration involved decreases in carboxylation efficiency and RuBP regeneration capacity. No clear evidence for a redistribution of nitrogen within the leaf was observed. Down-regulation of photosynthesis increased as the growing season progressed and appeared to be related to the source-sink balance of the trees. Analysis of the main leaf components revealed that the reduction in photosynthetic capacity was accompanied by an accumulation of starch in leaves (100%), which was probably responsible for the reduction in Rubisco activity (27%) and to a lesser extent for reductions in other photosynthetic components: chlorophyll (10%), soluble protein (9%), and N concentrations (12%) expressed on an area basis. Despite a 21% reduction in stomatal conductance in response to the elevated CO_2 treatment, stomatal limitation was significantly less in the elevated, than in the ambient, CO_2 treatment. Thus, after four growing seasons exposed to an elevated CO_2 concentration in the field, the trees maintained increased photosynthetic rates, although their photosynthetic capacity was reduced compared with trees grown in ambient CO_2 .

KEYWORDS: ELEVATED CARBON-DIOXIDE, FOLIAR GAS-EXCHANGE, GROWTH, LEAF, *PINUS TAEDA L.*, PLANTS, RESPONSES, RUBISCO, SINK REGULATION, STOMATAL CONDUCTANCE

1982

Rey, P., F. Eymery, and G. Peltier. 1990. Effects of CO₂-enrichment and of aminoacetonitrile on growth and photosynthesis of photoautotrophic calli of *Nicotiana glauca*. *Plant Physiology* 93(2):549-554.

1983

Reyenga, P.J., S.M. Howden, H. Meinke, and G.M. McKeon. 1999. Modelling global change impacts on wheat cropping in south-east Queensland, Australia. *Environmental Modelling & Software* 14(4):297-306.

The wheat module, I-WHEAT, from the APSIM cropping system model was used to investigate the impacts of changes in atmospheric CO₂ concentrations on wheat crops by modifying radiation use efficiency, transpiration efficiency, specific leaf area and critical nitrogen concentrations. The effects of several combinations of atmospheric CO₂, climate change and crop adaptation strategies on wheat production in the Burnett region were studied. Mean wheat yields were increased under doubled CO₂, with the response relative to ambient CO₂ greatest in dry years. Higher temperatures under the climate change scenarios moderated the yield gains achieved with increasing CO₂ and in some instances reversed them under the reduced rainfall scenario. The status of the region as a producer of prime hard wheat may be at risk due to reduced grain protein levels under doubled CO₂ and the increased likelihood of "heat shock" in the climate scenarios used. (C) 1999 Elsevier Science Ltd. All rights reserved.

KEYWORDS: AMBIENT ATMOSPHERE, ATMOSPHERIC CO₂ CONCENTRATIONS, CARBON-DIOXIDE ENRICHMENT, ELEVATED CO₂, HEAT-SHOCK, PLANT GROWTH, PROTEIN ACCUMULATION, RESPONSES, TEMPERATURE, WATER-USE EFFICIENCY

1984

Reynolds, J.F., J.L. Chen, P.C. Harley, D.W. Hilbert, R.L. Dougherty, and J.D. Tenhunen. 1992. Modeling the effects of elevated CO₂ on plants - extrapolating leaf response to a canopy. *Agricultural and Forest Meteorology* 61(1-2):69-94.

The response of canopies to short-duration exposure to elevated CO₂ was examined by using a detailed submodel of single-leaf ps exchange combined with a model of canopy structure and light penetration. The leaf model included a mechanistic ps exchange model and leaf energy balance equations, and the canopy model included a detailed description of spatial variability in environmental conditions within the canopy. The structure of the canopy model was designed to facilitate implementation of different leaf aggregation schemes. To compare six aggregation methods of increasing simplicity, daily carbon gain, and water use were simulated for *Quercus coccifera* under current ambient and future doubled CO₂. Analyses of simulated canopy responses confirmed the importance of including (1) leaf energy balance and (2) distinguishing between sunlit and shaded leaves. A multi-layer canopy model with Gaussian integration for sunlit leaves and a single leaf class for shaded leaves in each layer gave excellent results. A multi-layer model with one shaded and one sunlit leaf class gave a reasonable approximation, and the single-layer model with one sunlit and one shaded leaf class resulted in errors of up to 15%. Vertical gradients in leaf nitrogen content and leaf and stem area index had greater effects on canopy assimilation and transpiration than did gradients of stem or leaf inclination or leaf width. However, predictions of the relative response of CO₂ assimilation and transpiration to doubled CO₂ are rather robust and were not greatly affected by simplifications of the canopy model.

KEYWORDS: ALLOCATION, C-3, CARBON DIOXIDE, CLIMATE, ECOSYSTEMS, ENRICHMENT, GROWTH, NITROGEN, PHOTOSYNTHESIS, WATER-USE

1985

Rice, C.W., F.O. Garcia, C.O. Hampton, and C.E. Owensby. 1994. Soil microbial response in tallgrass prairie to elevated CO₂. *Plant and Soil* 165(1):67-74.

Terrestrial responses to increasing atmospheric CO₂ are important to the global carbon budget. Increased plant production under elevated CO₂ is expected to increase soil C which may induce N limitations. The objectives of this study were to determine the effects of increased CO₂ on 1) the amount of carbon and nitrogen stored in soil organic matter and microbial biomass and 2) soil microbial activity. A tallgrass prairie ecosystem was exposed to ambient and twice-ambient CO₂ concentrations in open-top chambers in the field from 1989 to 1992 and compared to unchambered ambient CO₂ during the entire growing season. During 1990 and 1991, N fertilizer was included as a treatment. The soil microbial response to CO₂ was measured during 1991 and 1992. Soil organic C and N were not significantly affected by enriched atmospheric CO₂. The response of microbial biomass to CO₂ enrichment was dependent upon soil water conditions. In 1991, a dry year, CO₂ enrichment significantly increased microbial biomass C and N. In 1992, a wet year, microbial biomass C and N were unaffected by the CO₂ treatments. Added N increased microbial C and N under CO₂ enrichment. Microbial activity was consistently greater under CO₂ enrichment because of better soil water conditions. Added N stimulated microbial activity under CO₂ enrichment. Increased microbial N with CO₂ enrichment may indicate plant production could be limited by N availability. The soil system also could compensate for the limited N by increasing the labile pool to support increased plant production with elevated atmospheric CO₂. Longer-term studies are needed to determine how tallgrass prairie will respond to increased C input.

KEYWORDS: ATMOSPHERIC CO₂, BIOMASS, CARBON DIOXIDE, DYNAMICS, ECOSYSTEMS, ENRICHMENT, GRASSLAND SOILS, MODEL, NITROGEN, ORGANIC-MATTER

1986

Riedo, M., D. Gyalistras, A. Fischlin, and J. Fuhrer. 1999. Using an ecosystem model linked to GCM-derived local weather scenarios to analyse effects of climate change and elevated CO₂ on dry matter production and partitioning, and water use in temperate managed grasslands. *Global Change Biology* 5(2):213-223.

Local effects of climate change (CC) and elevated CO₂ (2 x CO₂, 660 μmol mol⁻¹) on managed temperate grasslands were assessed by forcing a dynamic ecosystem model with weather scenarios. The aims of the study were to compare the relative importance of individual and combined effects of CC, 2 x CO₂, and photosynthetic acclimation, and to assess the importance of local site conditions. The model was driven by hourly means for temperature (T), precipitation (P), global radiation (G), vapour pressure (VP), and wind speed (U). Local climate scenarios were derived by statistical downscaling techniques from a 2 x CO₂ simulation with the General Circulation Model of the Canadian Climate Centre (CCC-GCMII). Simulations over 14 growing seasons to account for year-to-year variability of climate were carried out for a low, relatively dry site, and a high, more humid site. At both sites, shoot dry matter responded positively to 2 x CO₂ with the site at low elevation being more sensitive than the higher site. The effect of assumed changes in climate was negative at the lower, but positive at the higher site. Shoot dry matter was more sensitive to the effects of 2 x CO₂ than to CC. Both effects combined increased shoot dry matter by up to 20%. This was attributed to direct effects of 2 x CO₂ and increased T, and indirect stimulation via increased soil N availability. Biomass partitioning to roots increased with 2 x CO₂ but decreased with CC, while an intermediate response resulted from the combination. Leaf area index (LAI) increased under 2 x CO₂, but not enough to compensate fully for a decrease in leaf conductance. Under the 2 x CO₂ scenario

evapotranspiration (ET) decreased, but increased under CC. Photosynthetic acclimation reduced the effect of 2 x CO₂ on shoot growth, but had little effect on ET. The seasonal water use efficiency (WUE) was improved under 2 x CO₂, and reduced under CC. With the combination of both factors, the change was small but still positive, especially at the high elevation site with more favourable soil water conditions. This reflects the stronger positive yield response in combination with a smaller increase in ET under cooler, more humid conditions. The results for the combination of factors suggest that except for shoot growth, effects of 2 x CO₂ and CC tend to offset each other. While CC determines the sign of the ET response, the sign of the biomass response is determined by 2 x CO₂. The results highlight the importance of a site-specific analysis of ecosystem responses by using a flexible approach based on a combination of state-of-the-art downscaling, spatially resolved data sets, and a mechanistic model to obtain quantitative and reproducible assessments of climate change impacts at the ecosystem level.

KEYWORDS: ATMOSPHERIC CO₂, DAILY PRECIPITATION, GENERAL-CIRCULATION MODEL, GROWTH, LOLIUM-PERENNE L, RESPONSES, ROOT, SENSITIVITY ANALYSIS, SIMULATION, TRIFOLIUM-REPENS L

1987

Riedo, M., D. Gyalistras, A. Grub, M. Rosset, and J. Fuhrer. 1997. Modelling grassland responses to climate change and elevated CO₂. *Acta Oecologica-International Journal of Ecology* 18(3):305-311.

A mechanistic model for productive grassland was used to simulate the annual production of above-and belowground plant biomass in relation to fluxes of C, N, and water, and to test the sensitivity of yield, shoot/root ratio, evapotranspiration, and water use efficiency (WUE) to climate change scenarios (CC) and to elevated CO₂ (2 x CO₂) with or without consideration of photosynthetic acclimation of the plants. Validation with data from two Swiss sites revealed satisfactory agreement between simulation and measurement for yield, energy fluxes, and N- dynamics. Local weather scenarios were derived from the results of two General Circulation Models (GCM) for 2 x CO₂ by a statistical down-scaling procedure. Biomass production changed by a maximum of 8% in response to CC without 2 x CO₂ effects, by 1-17% in response to 2 x CO₂ alone, and by 6-20% in response to the combination of CC and 2 x CO₂. With plant acclimation, biomass Production increased only up to 8% with elevated CO₂, as compared to a maximum increase of 20% in the absence of plant acclimation. Reduced yield with CC was obtained for sites with low soil water holding capacity. Decreased evapotranspiration and increased WUE with 2 x CO₂ were partially offset by CC. The simulations indicated that productivity of managed grassland is sensitive to different assumptions about changes in climate, CO₂ concentration, and photosynthetic acclimation, and that the effects of elevated CO₂ are modified by CC and depend on local soil conditions.

KEYWORDS: CARBON, GENERAL-CIRCULATION MODEL, SOIL

1988

Righetti, B., E. Magnanini, and F. Rossi. 1993. Photosynthetic carbon-dioxide uptake and oxygen accumulation during in-vitro culture of actinidia-deliciosa CV tomuri. *Environmental and Experimental Botany* 33(4):523-528.

Proliferating cultures of Actinidia deliciosa cv Tomuri were grown in vitro under a photosynthetic photon flux density (PPFD) of 120 μmol m²/s. Some jars were daily enriched with 2000 μmol/l CO₂ administered at the end of the dark period. Head space analysis revealed that CO₂ accumulated up to 9500 μmol/l during the dark period and was drastically reduced by photosynthetic activity to 150-200 μmol/l during the

photoperiod without any significant difference between CO₂-enriched and non-enriched cultures. Oxygen concentration assayed at the end of the photoperiod showed a steady increase during the 44 days of culture and was not reduced to atmospheric values by respiratory processes during the dark period. CO₂ enrichment enhanced O₂ production and accumulation to 32.5% at the end of the culture period. Oxygen photoreduction and its photo-oxidative damage to green tissue cells are discussed.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO₂, ENRICHMENT, EXCHANGE, GROWTH, LIGHT, PLANTS, STARCH, STRESS, TOXICITY

1989

Righetti, B., D.M. Reid, and T.A. Thorpe. 1996. Growth and tissue senescence in Prunus avium shoots grown in vitro at different CO₂/O₂ ratios. *In Vitro Cellular & Developmental Biology-Plant* 32(4):290-294.

The rate of metabolism and biosynthetic processes make in vitro cultures very sensitive to environmental changes, and therefore subject to physiological and morphological alterations leading to senescence in the short term. The effects of three different calibrated atmospheric compositions were studied during in vitro culture of Prunus avium shoots. At 0.034% CO₂-21% O₂ (vol/vol), which stimulate the natural atmosphere, the highest growth rate and chlorophyll content were recorded. When grown at 0.09% CO₂-8% O₂ (vol/vol), a favorable condition for photosynthesis and growth, cultures showed a higher percentage of dry matter and elevated ethylene production, but total chlorophyll was lower. These shoots were also highly lignified and fibrous with red pigmentation along the leaves and stems. At 0% CO₂-21% O₂ (vol/vol), in contrast, growth and ethylene formation were inhibited; chlorophyll content was lowest in comparison with the other two environmental conditions, but greening of tissues was observed after the first half of the culture period. Senescence symptoms, as indicated by decreased chlorophyll, appeared after about 18 d of culture for tissues grown in CO₂-containing atmospheres. These experiments provided evidence that in CO₂-enriched cultures biomass production steadily increased even when chlorophyll decreased. A possible role of CO₂ in promoting tissue-senescence through activation of photooxidative events and ethylene synthesis is discussed.

KEYWORDS: ACTIVATION, BEAN-LEAVES, CARBON DIOXIDE, CO₂- ENRICHMENT, CROP RESPONSES, LONG-TERM ACTION, NET PHOTOSYNTHETIC RATE, OXYGEN CONCENTRATION, PHOTORESPIRATION, TOXICITY

1990

Rigler, E., and S. Zechmeister-Boltenstern. 1998. Influence of nitrogen and carbon dioxide on ethylene and methane production in two different forest soils. *Microbiological Research* 153(3):227-237.

The impact of nitrogen and CO, on ethylene and methane production was investigated in two different forest soils. The soils were adjusted to a water tension of 30 kPa. Nitrogen was added in the form of KNO₃ or (NH₄)(2)SO₄ and CO₂ was added in 5 different concentrations. To half of the samples, C₂H₂ was added to inhibit ethylene uptake. After 0, 24, and 96 hours, ethylene and methane concentrations were measured by gas chromatography. Ethylene net production increased with increasing N and CO₂ concentrations. In the presence of acetylene, ethylene production was unaffected by the investigated amendments. Therefore, we suppose that the increasing ethylene net production rates are due to decreasing ethylene uptake rates. In the deciduous forest soil, there was no ethylene net production rate, as uptake rates exceeded production rates. Methane net production rates in the spruce forest soil increased with increasing N additions possibly due to a lowered C:N ratio and a decreased methane oxidation. Ethylene production rates in the presence

of acetylene were slightly enhanced. In the deciduous forest soil, methane uptake rates decreased with nitrogen possibly due to the inhibition of the methanomonooxygenase. CO₂ seemed to increase methane production in the presence of acetylene but had no significant effect on methane net production. Acetylene might serve as a substrate for methanogenesis.

KEYWORDS: ACCUMULATION, ACETYLENE-REDUCTION ASSAY, BIOSYNTHESIS, CONSUMPTION, FERTILIZERS, INHIBITION, MICROORGANISMS, NADH-FE(III)EDTA OXIDOREDUCTASE, NITRATE, RESPONSES

1991

Rigler, E., and S. Zechmeister-Boltenstern. 1999. Oxidation of ethylene and methane in forest soils - effect of CO₂ and mineral nitrogen. *Geoderma* 90(1-2):147-159.

The influence of inorganic nitrogen and CO₂ on microbial C₂H₄ and CH₄ consumption was evaluated in two forest soils (montane spruce forest and colline deciduous forest) under laboratory conditions at 25 degrees C. The soils were adjusted to a water tension of - 30 kPa. Nitrogen was added as KNO₃ or (NH₄)₂SO₄, while CO₂ enrichment ranged from 1-20%. At 0, 24, and 96 h, the amounts of CH₄ and C₂H₄ consumed were determined. In both soils, we observed a parallel response of C₂H₄ and CH₄ to all kinds and concentrations of amendments, plausibly due to co- metabolism of C₂H₄ by either methanotrophs or nitrifiers. Ammonium-N inhibited hydrocarbon oxidation in the deciduous forest soil, but promoted it in the acidic spruce forest soil. Ammonium addition narrowed the C:N ratio of the spruce forest soil which was characterized by low pH but high humus content. Therefore, the general living conditions for microorganisms might have been improved. Conversely, NO₃- inhibited hydrocarbon oxidation in both soils, here a non-specific ion toxicity ('salt-effect') is discussed. CO₂ also had an inhibitory effect on hydrocarbon microbial uptake at high concentrations, with its production increasing at elevated CO₂ levels. We conclude that the impact of nitrogen inputs and of enhanced CO₂ on the sink strength for hydrocarbons depends on the amount and the kind of addition as well as on soil type. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: AMMONIUM INHIBITION, ATMOSPHERIC METHANE, BACTERIA, CAPACITY, CONSUMPTION, HYDROCARBONS, METABOLISM, N-FERTILIZATION, NITRIFICATION, TEMPERATURE

1992

Riis, T., and K. Sand-Jensen. 1997. Growth reconstruction and photosynthesis of aquatic mosses: Influence of light, temperature and carbon dioxide at depth. *Journal of Ecology* 85(3):359-372.

1 The mosses *Sphagnum subsecundum* and *Drepanocladus exannulatus* dominate the vegetation in the oligotrophic, softwater Lake Grane Langso, Denmark, even at great depths where light and temperature are low. We used seasonal changes in morphology to reconstruct the annual growth and the longevity of the mosses and measurements of photosynthesis and respiration to evaluate the importance of light, temperature and CO₂ for the growth patterns at depth in the lake. 2 The reconstruction technique revealed that the mosses had a relatively fast growth rate (90- 250 mm shoot(-1) year(-1)) and were short lived (0.7- 2.9 years). The shoots of both moss species grew faster in deep than in shallow water. Growth experiments in summer confirmed that *Sphagnum* grew more slowly and decayed more rapidly in shallow than in deep water. 3 Fast growth of mosses in deep waters can be accounted for by lower temperature, extensive CO₂ supersaturation and nutrient enrichment in the hypolimnion during summer stratification. Maximum rate of light-saturated photosynthesis in July was 3.3-fold higher and of

dark respiration 1.3-fold lower in *Sphagnum* from 9.5m incubated at the ambient 8 degrees C than in *Sphagnum* from 0.7m incubated at 20 degrees C. The net daily carbon fixation was greater in deep than in shallow water despite the much lower irradiance at depth. Extensive CO₂ supersaturation stimulated photosynthesis several-fold relative to the rates observed in air-saturated water. Tissues of *Sphagnum* were richer in nitrogen in deep than in shallow water during summer, but the importance of nutrient availability to annual moss growth remains unclear. 4 Reconstruction techniques are recommended for comparative studies on annual and interannual growth patterns of mosses within lakes and among lakes of different altitude, latitude and water chemistry. This information can be based on just a single collection and can therefore include remote sites with adverse climate.

KEYWORDS: ANTARCTIC LAKES, BENTHIC PLANTS, FONTINALIS-ANTIPYRETICA, IRRADIANCE, MACROPHYTE COMMUNITIES, POPULATION-DYNAMICS, PRODUCTION ECOLOGY, STRATEGIES, SWEDISH LAPLAND, TUNDRA PLANTS

1993

Rillig, M.C., and M.F. Allen. 1998. Arbuscular mycorrhizae of *Gutierrezia sarothrae* and elevated carbon dioxide: Evidence for shifts in C allocation to and within the mycobiont. *Soil Biology and Biochemistry* 30(14):2001-2008.

In a complete 2 x 2 factorial greenhouse experiment we examined the responses of arbuscular mycorrhizal (AM) and non- mycorrhizal fungi to *Gutierrezia sarothrae* shrubs grown in elevated atmospheric carbon dioxide (750 μ l l(-1)) and fertilized with N. AM percent infection did not change significantly with elevated CO₂, but arbuscular infection increased 14-fold in the low-N treatment. Extraradical hyphal length increased on an absolute basis in elevated CO₂, and also per infected root length. In the high-N treatments, increasing CO₂ caused a decrease in hyphal length per infected root length, and an increase in vesicular infection. There was a significant positive response of AM infection intensity to increasing CO₂ for the high N treatment, and a similar trend in the low N treatment. Infection intensity was positively correlated with arbuscular infection and with vesicular infection. Nonmycorrhizal fungi did not respond to any of the treatment combinations, as measured by percent root infection and external hyphal length. Our results indicate that C allocation to the AM fungi was increased in elevated CO₂, and that the mycobiont in turn increased C allocation to external hyphae. (C) 1998 Elsevier Science Ltd. All rights reserved.

KEYWORDS: ATMOSPHERIC CO₂, COLONIZATION, ENRICHMENT, FUNGI, HYPHAE, RESPONSES, RHIZOSPHERE, ROOTS, SOIL

1994

Rillig, M.C., and M.F. Allen. 1999. What is the role of arbuscular mycorrhizal fungi in plant-to- ecosystem responses to Elevated atmospheric CO₂? *Mycorrhiza* 9(1):1-8.

We advocate the concept of an arbuscular mycorrhiza (AM) as a temporally and spatially complex symbiosis representing a suite of hosts and fungi, as against the more traditional "dual organism" view. We use the hierarchical framework presented in Fig. 1 as a basis for organizing many unanswered questions, and several questions that have not been asked, concerning the role of AM in responses to elevated atmospheric CO₂. We include the following levels: plant host, plant population, plant community, functional group and ecosystem. Measurements of the contributions of AM fungi at the various levels require the use of different response variables. For example, hyphal nutrient translocation rates or percent AM root infection may be important measures at the individual plant level, but hyphal biomass or glomalin production and turnover are more relevant at the ecosystem level. There is a discrepancy

between our knowledge of the multifaceted role of AM fungi in plant and ecosystem ecology and most of the current research aimed at elucidating the importance of this symbiosis in global-change scenarios. Our framework for more integrated and multifactorial research on mycorrhizal involvement in regulating CO₂ responses may also serve to enhance communication between researchers working at different scales on large global-change ecosystem projects.

KEYWORDS: BIOMASS PRODUCTION, BOUTELOUA-GRACILIS, CARBON DIOXIDE, COLONIZATION, LITTER DECOMPOSITION, ROOTS, SOIL BIOTA, SYMBIOTIC N-2 FIXATION, TRIFOLIUM-REPENS L, WATER RELATIONS

1995

Rillig, M.C., M.F. Allen, J.N. Klironomos, N.R. Chiariello, and C.B. Field. 1998. Plant species-specific changes in root-inhabiting fungi in a California annual grassland: responses to elevated CO₂ and nutrients. *Oecologia* 113(2):252-259.

Five co-occurring plant species from an annual mediterranean grassland were grown in monoculture for 4 months in pots inside open-top chambers at the Jasper Ridge Biological Preserve (San Mateo County, California). The plants were exposed to elevated atmospheric CO₂ and soil nutrient enrichment in a complete factorial experiment. The response of root-inhabiting non-mycorrhizal and arbuscular mycorrhizal fungi to the altered resource base depended strongly on the plant species. Elevated CO₂ and fertilization altered the ratio of non-mycorrhizal to mycorrhizal fungal colonization for some plant species, but not for others. Percent root infection by non-mycorrhizal fungal increased by over 500% for *Linanthus parviflorus* in elevated CO₂, but decreased by over 80% for *Bromus hordeaceus*. By contrast, the mean percent infection by mycorrhizal fungi increased in response to elevated CO₂ for all species, but significantly only for *Avena barbata* and *B. hordeaceus*. Percent infection by mycorrhizal fungi increased, decreased, or remained unchanged for different plant hosts in response to fertilization. There was evidence of a strong interaction between the two treatments for some plant species and non-mycorrhizal and mycorrhizal fungi. This study demonstrated plant species- and soil fertility-dependent shifts in belowground plant resource allocation to different morphogroups of fungal symbionts. This may have consequences for plant community responses to elevated CO₂ in this California grassland ecosystem.

KEYWORDS: AMMONIUM-SULFATE, ARBUSCULAR MYCORRHIZAL FUNGI, ATMOSPHERIC CARBON-DIOXIDE, COLONIZATION, COMMUNITIES, ENRICHMENT, FEEDBACK, INFECTION, NITRATE, RHIZOSPHERE

1996

Rillig, M.C., M.F. Allen, J.N. Klironomos, and C.B. Field. 1998. Arbuscular mycorrhizal percent root infection and infection intensity of *Bromus hordeaceus* grown in elevated atmospheric CO₂. *Mycologia* 90(2):199-205.

Using *Bromus hordeaceus*, a grass from a Mediterranean annual grassland in California, we measured changes in infection intensity, rather than the more traditional % root infection, as an indicator of response to elevated atmospheric CO₂ and soil nutrient enrichment. Intensity was measured as the number of intraradical hyphae intersecting a microscope cross-hair for specific root diameter size classes. We found an increase in intensity of infection when plants were exposed to elevated CO₂, and we found a decrease in infection intensity when plants were fertilized. This finding is significant in that it provides evidence for an increase in carbon allocation to the mycobiont under elevated CO₂ even in the absence of change in percent infection, or mycorrhizal root length. Previous studies may therefore have overlooked an important response of arbuscular mycorrhizal fungi to this treatment,

leading to an underestimation of the importance of mycorrhizae under elevated CO₂. Infection intensity may also change in response to many other treatments and environmental variables that the symbiosis is exposed to, highlighting the potential usefulness of intensity as a response variable in mycorrhizal research.

KEYWORDS: CARBON, COLONIZATION, COTTON, ENRICHMENT, PHOTOSYNTHESIS, PLANTS, RESPONSES, RHIZOSPHERE

1997

Rillig, M.C., C.B. Field, and M.F. Allen. 1999. Fungal root colonization responses in natural grasslands after long-term exposure to elevated atmospheric CO₂. *Global Change Biology* 5(5):577-585.

Arbuscular mycorrhizae, ubiquitous mutualistic symbioses between plant roots and fungi in the order Glomales, are believed to be important controllers of plant responses to global change, in particular to elevated atmospheric CO₂. In order to test if any effects on the symbiosis can persist after long-term treatment, we examined root colonization by arbuscular mycorrhizal (AM) and other fungi of several plant species from two grassland communities after continuous exposure to elevated atmospheric CO₂ for six growing seasons in the field. For plant species from both a sandstone and a serpentine annual grassland there was evidence for changes in fungal root colonization, with changes occurring as a function of giant host species. We documented decreases in percentage nonmycorrhizal fungal root colonization in elevated CO₂ for several plant species. Total AM root colonization (%) only increased significantly for one out of the five plant species in each grassland. However, when dividing AM fungal hyphae into two groups of hyphae (fine endophyte and coarse endophyte), we could document significant responses of AM fungi that were hidden when only total percentage colonization was measured. We also documented changes in elevated CO₂ in the percentage of root colonized by both AM hyphal types simultaneously. Our results demonstrate that changes in fungal root colonization can occur after long-term CO₂ enrichment, and that the level of resolution of the study of AM fungal responses may have to be increased to uncover significant changes to the CO₂ treatment. This study is also one of the first to document compositional changes in the AM fungi colonizing roots of plants grown in elevated CO₂. Although it is difficult to relate the structural data directly to functional changes, possible implications of the observed changes for plant communities are discussed.

KEYWORDS: ARBUSCULAR MYCORRHIZAL FUNGI, BOUTELOUA-GRACILIS, ENRICHMENT, GROWTH, INFECTION, SYSTEM, TREE

1998

Rillig, M.C., C.B. Field, and M.F. Allen. 1999. Soil biota responses to long-term atmospheric CO₂ enrichment in two California annual grasslands. *Oecologia* 119(4):572-577.

Root, arbuscular-mycorrhizal (AM), soil faunal (protozoa and microarthropods), and microbial responses to field exposure to CO₂ for six growing seasons were measured in spring 1997 in two adjacent grassland communities. The grasslands showed contrasting root responses to CO₂ enrichment: whereas root length was not affected in the sandstone grassland, it was greater in the serpentine grassland, as was specific root length. AM fungal hyphal lengths were greater in the sandstone, but were unaffected in the serpentine community. This lent support to the hypothesis that there may be a tradeoff in resource allocation to more fine roots or greater mycorrhizal extraradical hyphal length. AM root infection was greater in both communities at elevated CO₂, as was the proportion of roots containing arbuscules. Our data on total hyphal lengths, culturable and active fungi, bacteria, and protozoa supported the hypothesis that the fungal food chain was more strongly stimulated than the bacterial chain. This study is one of the first to test

these hypotheses in natural multi-species communities in the field.

KEYWORDS: ARBUSCULAR MYCORRHIZAL FUNGI, CARBON DIOXIDE, COMMUNITIES, ECOSYSTEMS, ELEVATED CO₂, GROWTH, PASTURE, RHIZOSPHERE, SYSTEMS, TALLGRASS PRAIRIE

1999

Rillig, M.C., K.M. Scow, J.N. Klironomos, and M.F. Allen. 1997. Microbial carbon-substrate utilization in the rhizosphere of *Gutierrezia sarothrae* grown in elevated atmospheric carbon dioxide. *Soil Biology and Biochemistry* 29(9-10):1387-1394.

Differences in rhizosphere microbial community function in response to *Gutierrezia sarothrae* plants grown in elevated CO₂ (750 μ l l⁻¹) and fertilized with nitrogen were studied using the Biolog microplate analysis of sole C substrate utilization. Compared to ambient CO₂ under elevated CO₂, polymers were more slowly oxidized by the microbial community, amides showed no change in usage, and all other substrate groups were more rapidly utilized, although there was no significant change in the number of viable bacteria. No microbial community responses to N fertilization were detected. The results indicate that potential functional changes in the soil microbial community in response to elevated CO₂ have to be taken into account in future experiments. Differential use of rhizo-deposits in elevated CO₂ may have important consequences for biogeochemistry and plant growth. (C) 1997 Elsevier Science Ltd.

KEYWORDS: CO₂, COMMUNITIES, DECOMPOSITION, DIVERSITY, FEEDBACK, LEAF LITTER, PATTERNS, RESPONSES, ROOTS

2000

Ringelberg, D.B., J.O. Stair, J. Almeida, R.J. Norby, E.G. O'Neill, and D.C. White. 1997. Consequences of rising atmospheric carbon dioxide levels for the belowground microbiota associated with white oak. *Journal of Environmental Quality* 26(2):495-503.

The consequences for belowground microbiota under conditions of rising atmospheric CO₂ are largely unknown. In this research we examined the microbiota associated with white oak (*Quercus alba* L.). It was our hypothesis that an increase in CO₂ level would induce a change in the rhizosphere-associated microbial abundance and community composition. To provide an in situ estimation of microbial abundance and community composition, ester-linked polar lipid fatty acid (PLFA) technology was utilized. This technology, based on the quantitative measurement of membrane lipid fatty acids, has been utilized in the accurate identification and description of bacterial isolates and communities. Initial experiments demonstrated that a clear distinction in lipid patterns and microbial biomass existed between sterile roots and those of roots containing an associated viable microbiota. Statistical approaches were then used to determine what differences existed between individual PLFA and PLFA patterns obtained from white oak fine roots and bulk soils. An analysis of variance (ANOVA) showed significant differences to exist in the relative percentages of individual prokaryotic PLFA collected under ambient vs. elevated CO₂ and between those associated with fine roots and bulk soils. Multivariate statistics showed distinct differences in the patterns of prokaryotic PLFA detected in the rhizosphere vs. the surrounding bulk soil, but did not identify differences related to elevated CO₂ exposures. An artificial neural network recognized PLFA patterns unique to three different CO₂ exposures: similar to 35, similar to 50, and similar to 65 Pa. Results of the three statistical tests were viewed as supportive of the hypothesis describing significant differences in individual PLFA and patterns of PLFA as a result of elevated CO₂ exposure.

KEYWORDS: BIOMASS, ELEVATED CO₂, ENRICHMENT, FATTY-

ACIDS, GROWTH, MYCORRHIZAL COLONIZATION, PLANT-RESPONSES, POLYBETA HYDROXYBUTYRATE, QUERCUS-ALBA, RHIZOSPHERE

2001

RiviereRolland, H., P. Contard, and T. Betsche. 1996. Adaptation of pea to elevated atmospheric CO₂: Rubisco, phosphoenolpyruvate carboxylase and chloroplast phosphate translocator at different levels of nitrogen and phosphorus nutrition. *Plant, Cell and Environment* 19(1):109-117.

Resource allocation in high CO₂ was studied with respect to plant nutrition. Pea (*Pisum sativum*) was grown in CO₂-enriched air (1000 cm³ m⁻³ CO₂) during the entire vegetative phase, or grown in ambient air (340 cm³ m⁻³ CO₂), with different levels of nitrogen or phosphorus supply. Rubisco specific activity, abundance and small subunit transcript levels were unaltered at high N but declined at reduced N depending upon the degree of N deprivation. It is proposed that (a) a threshold value for the N status occurs in pea above which Rubisco is not down-regulated by high CO₂ and (b) a high leaf level of soluble carbohydrates is not a sufficient condition to down-regulate Rubisco in high CO₂. Phosphoenolpyruvate (PEP) carboxylase decreased, and chloroplast phosphate (P)- translocator increased, in high CO₂. In contrast to Rubisco, down-regulation of PEP carboxylase was alleviated by low N and enhanced by low P. The increase in the P-translocator was little affected by N but was accentuated by low P. The increase in the P-translocator is considered to be one way of alleviating low P conditions in the chloroplast and thus re-balancing carbon partitioning between starch and soluble carbohydrates and amino acids. It is proposed that acclimation of PEP carboxylase and P-translocator reflects adaptation to metabolic perturbations caused by high CO₂.

KEYWORDS: ANTISENSE RBCS, C-3 PLANTS, CARBON DIOXIDE, CELLS, GROWTH, LIGHT, OXYGENASE, PHOTOSYNTHESIS, SINK REGULATION, TRIFOLIUM-SUBTERRANEUM L

2002

Robertz, P. 1999. Effects of long-term CO₂ enrichment and nutrient availability in Norway spruce. I. Phenology and morphology of branches. *Trees-Structure and Function* 13(4):188-198.

Branches of 30-year-old Norway spruce [*Picea abies* (L.) Karst.] trees were enclosed in ventilated, transparent plastic bags and flushed with air containing ambient (A approximate to 370 μ mol CO₂ mol⁻¹) or ambient plus 340 μ mol CO₂ mol⁻¹ (EL). Light-saturated photosynthesis was on average 56% higher in EL compared to A. Branch phenology and morphology were strongly related to nitrogen concentration (mg g⁻¹ dry mass) in the foliage and to elevated temperatures in the bags, but no direct effect of EL was found. In 1995, budbreak occurred on average 4 days earlier in the bags compared to the control branches, which was partly explained by the temperature elevation in the bags. No nutrient or EL effect on budbreak was found. Increases in temperature and nitrogen supply increased shoot growth: together they explained 76% of the variation in the extension rate, 63% of the variation in extension duration and 65% of the variation in final length of leading shoots. Shoot morphology was altered both by increased nitrogen availability and by the enclosure induced environmental changes inside the bags, leading to reduced mutual shading between needles. Specific needle area (SNA) was lower in EL, but this was related to lower nitrogen concentrations. Total dry mass of the branches was unaffected by EL. It is concluded that treating individual branches of Norway spruce with elevated CO₂ does not increase branch growth. The nutrient status of the branch and climate determine its growth, i.e., its sink strength for carbon. Increased export of carbohydrates to the rest of the tree is probable in EL treated branches.

KEYWORDS: *ABIES AMABILIS, CARBON DIOXIDE, ELEVATED CO₂, GROWTH, LOBLOLLY-PINE TREES, NET PHOTOSYNTHESIS, NUTRITION, PICEA-SITCHENSIS, RESPONSES, STOMATAL CONDUCTANCE*

2003

Roberntz, P., and S. Linder. 1999. Effects of long-term CO₂ enrichment and nutrient availability in Norway spruce. II. Foliar chemistry. *Trees-Structure and Function* 14(1):17-27.

Branches on 30-year-old Norway spruce trees [*Picea abies* (L.) Karst.] were exposed to ambient (AMB) or ambient plus 350 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ (EL) for 4 years (except winters), using the branch bag technique (BB). The trees were growing on plots with low (control) and high (irrigated-fertilised) availability of soil nutrients. The seasonal variation in foliar macronutrients and non-structural carbohydrates in current and 1-year-old shoots was monitored throughout the treatment period. When the branches were harvested at the end of treatment, macronutrients were analysed in five age classes of foliage. The concentration of all elements, except magnesium, generally increased in AMB, i.e. a 'bag effect', but decreased as an effect of EL, i.e. a 'CO₂ effect'. At the final harvest K, P, N and S were reduced in young needles by EL, whereas Mg was reduced in older needles on both plots. A change in needle morphology by EL possibly caused a dilution effect in irrigated-fertilised needles, but not in control needles. Reductions in K and Mg are suggested to be an effect of increased phloem transport from the branch, in consequence of higher rates of carbon fixation in EL. Foliage in BBs had higher concentration of Ca, but there was no significant effect of the EL-treatment, indicating that elevated CO₂ had no effect on stomatal conductance. Quinic acid concentration decreased, but shikimic acid concentration increased in BBs, independently of CO₂ treatment. Concentrations of starch and sugars increased in the EL-treatment, but pinitol decreased.

KEYWORDS: *ELEVATED ATMOSPHERIC CO₂, GROWTH, LEAF ANATOMY, LEAVES, NEEDLES, PLANTS, RESPONSES, SCOTS PINE, STOMATAL CONDUCTANCE, TREES*

2004

Roberntz, P., and J. Stockfors. 1998. Effects of elevated CO₂ concentration and nutrition on net photosynthesis, stomatal conductance and needle respiration of field-grown Norway spruce trees. *Tree Physiology* 18(4):233-241.

To study the effects of elevated CO₂ on gas exchange, nonstructural carbohydrate and nutrient concentrations in current-year foliage of 30-year-old Norway spruce (*Picea abies* (L.) Karst.) trees, branches were enclosed in ventilated, transparent plastic bags and flushed with ambient air (mean 370 $\mu\text{mol CO}_2 \text{ mol}^{-1}$; control) or ambient air + 340 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ (elevated CO₂) during two growing seasons. One branch bag was installed on each of 24 selected trees from control and fertilized plots. To reduce the effect of variation among trees, results from each treated branch were compared with those from a control branch on the same whorl of the same tree. Elevated CO₂ increased rates of light-saturated photosynthesis on average by 55% when measured at the treatment CO₂ concentration. The increase was larger in shoots with high needle nitrogen concentrations than in shoots with low needle nitrogen concentrations. However, shoots grown in elevated CO₂ showed a decrease in photosynthetic capacity compared with shoots grown in ambient CO₂. When measured at the internal CO₂ concentration of 200 $\mu\text{mol CO}_2 \text{ mol}^{-1}$, photosynthetic rates of branches in the elevated CO₂ treatments were reduced by 8 to 32%. The elevated CO₂ treatment caused a 9 to 20% reduction in carboxylation efficiency and an 18% increase in respiration rates. In response to elevated CO₂, starch, fructose and glucose concentrations in the needles increased on average 33%, whereas concentrations of potassium,

nitrogen, phosphorus, magnesium and boron decreased. Needle nitrogen concentrations explained 50-60% of the variation in photosynthesis and CO₂ acclimation was greater at low nitrogen concentrations than at high nitrogen concentrations. We conclude that the enhanced photosynthetic rates found in shoots exposed to elevated CO₂ increased carbohydrate concentrations, which may have a negative feedback on the photosynthetic apparatus and stimulate cyanide-resistant respiration. We also infer that the decrease in nutrient concentrations of needles exposed to elevated CO₂ was the result of retranslocation of nutrients to other parts of the branch or tree.

KEYWORDS: *ACCLIMATION, ATMOSPHERIC CO₂, ENRICHMENT, GAS-EXCHANGE, LEAVES, NITROGEN, PICEA, PINE, PLANTS, RISING CO₂*

2005

Roberts, S.W., W.C. Oechel, P.J. Bryant, S.J. Hastings, J. Major, and V. Nosov. 1998. A field fumigation system for elevated carbon dioxide exposure in chaparral shrubs. *Functional Ecology* 12(4):708-719.

1. Modifications and improvements in the hardware and software of a free-air CO₂ enrichment (FACE) system are described. The modifications were undertaken to minimize the amount of structure required and to improve software control of CO₂ set points. 2. A new low-cost CO₂ flow controller which provides increased reliability is described. 3. Analysis of system performance during a 79-day evaluation period of operation (13 h day⁻¹) showed that for 1 min averages, the system is capable of maintaining a 550 p.p.m. \pm 10% CO₂ set point during 78% of the operating time and a 550 p.p.m. \pm 20% set point during 95% of the operating time. Ten-minute averages were within \pm 10% and 20% during 87% and 96% of the operating time, respectively. 4. Continuous measurements of the spatial variation in CO₂ concentration inside the FACE ring over an 18-day period showed that of the total 16-m diameter treatment area, the central 11-m diameter portion remains within the 550 p.p.m. \pm 10% set point. 5. Daily course gas-exchange measurements in matched individuals of the chaparral shrub *Adenostoma fasciculatum* just prior to and following a 6-week fumigation period at 550 p.p.m. CO₂ in the FACE treatment ring showed the FACE plants with reduced photosynthetic rates and higher (less stressful) water potentials compared with control A. *fasciculatum* plants measured at the same times and conditions, indicating the responsiveness of this species to elevated CO₂ conditions.

KEYWORDS: *CO₂, DESIGN*

2006

Robertson, E.J., and R.M. Leech. 1995. Significant changes in cell and chloroplast development in young wheat leaves (triticum-aestivum CV hereward) grown in elevated CO₂. *Plant Physiology* 107(1):63-71.

Cell and chloroplast development were characterized in young *Triticum aestivum* cv Hereward leaves grown at ambient (350 $\mu\text{mol L}^{-1}$) or at elevated (650 $\mu\text{mol L}^{-1}$) CO₂. In elevated CO₂, cell and chloroplast expansion was accelerated by 10 and 25%, respectively, in the first leaf of 7-d-old wheat plants without disruption to the leaf developmental pattern. Elevated CO₂ did not affect the number of chloroplasts in relation to mesophyll cell size or the linear relationship between chloroplast number or size and mesophyll cell size. No major changes in leaf anatomy or in chloroplast ultrastructure were detected as a result of growth in elevated CO₂, but there was a marked reduction in starch accumulation. In leaf sections fluorescently tagged antisera were used to visualize and quantitate the amount of cytochrome f, the α - and β -subunits of the coupling factor 1 in ATP synthase, D1 protein of the photosystem II reaction center, the 33-kD protein of the extrinsic oxygen-evolving complex, subunit II of photosystem I, and ribulose-1,5-

bisphosphate carboxylase/oxygenase. A significant finding was that in 10 to 20% of the mesophyll cells grown in elevated CO₂ the 33-kD protein of the extrinsic oxygen-evolving complex of photosystem II and cytochrome f were deficient by 75%, but the other proteins accumulated normally.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO₂, CARBON DIOXIDE, CROP RESPONSES, ENRICHMENT, LEAF, LIGHT, PHOTOSYNTHESIS, PLANTS, PROTEIN

2007

Robertson, E.J., M. Williams, J.L. Harwood, J.G. Lindsay, C.J. Leaver, and R.M. Leech. 1995. Mitochondria increase 3-fold and mitochondrial proteins and lipid change dramatically in postmeristematic cells in young wheat leaves grown in elevated CO₂. *Plant Physiology* 108(2):469-474.

A dramatic stimulation in mitochondrial biogenesis during the very early stages of leaf development was observed in young wheat plants (*Triticum aestivum* cv Hereward) grown in elevated CO₂ (650 μ mol L⁻¹). An almost 3-fold increase in the number of mitochondria was observed in the very young leaf cells at the base of the first leaf of a 7-d-old wheat plant. In the same cells large increases in the accumulation of a mitochondrial chaperonin protein and the mitochondrial 2-oxoglutarate dehydrogenase complex and pyruvate dehydrogenase complex were detected by immunolabeling. Furthermore, the basal segment also shows a large increase in the rate of radiolabeling of diphosphatidylglycerol, a lipid confined to the inner mitochondrial membrane. This dramatic response in very young leaf cells to elevated CO₂ suggests that the numerous documented positive effects of elevated CO₂ on wheat leaf development are initiated as early as 12 h postmitosis.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, LOCALIZATION, PHOTOSYNTHESIS, RESPIRATION

2008

Robertson, G.P. 1999. Effect on the biosphere of elevated atmospheric CO₂. *Science* 285(5435):1852.

2009

Robinson, C.H., A. Michelsen, J.A. Lee, S.J. Whitehead, T.V. Callaghan, M.C. Press, and S. Jonasson. 1997. Elevated atmospheric CO₂ affects decomposition of *Festuca vivipara* (L) Sm litter and roots in experiments simulating environmental change in two contrasting arctic ecosystems. *Global Change Biology* 3(1):37-49.

Mass loss, together with nitrogen and carbon loss, from above-ground material and roots of *Festuca vivipara* were followed for 13 months in a high Arctic polar semidesert and a low Arctic tree-line dwarf shrub heath. *Festuca vivipara* for the study was obtained from plants cultivated at two different CO₂ concentrations (350 and 500 μ mol L⁻¹) in controlled environment chambers in the UK. Each of the four resource types (shoots or roots from plants grown in elevated or ambient CO₂ concentrations) was subsequently placed in an experiment simulating aspects of environmental change in each Arctic ecosystem. Air, litter and soil temperatures were increased using open-topped polythene tents at both sites, and a 58% increase in summer precipitation was simulated at the high Arctic site. Mass loss was greatest at the low Arctic site, and from the shoot material, rather than the roots. Shoots grown under an elevated CO₂ concentration decomposed more slowly at the high Arctic site, and more quickly at the low Arctic one, than shoots grown at ambient CO₂. After 13 months, greater amounts of C and N remained in above-ground litter from plants grown under elevated, rather than

ambient, CO₂ at the polar semi-desert site, although lower amounts of C remained in elevated CO₂ litter at the low Arctic ecosystem. In the high Arctic, roots grown in the 500 μ mol L⁻¹ CO₂ concentration decomposed significantly more slowly than below-ground material derived from the ambient CO₂ chambers. Elevated CO₂ concentrations significantly increased the initial C:N ratio, % soluble carbohydrates and alpha-cellulose content, and significantly decreased the initial N content, of the above-ground material compared to that derived from the ambient treatment. Initially, the C:N ratio and percentage N were similar in both sets of roots derived from the two different CO₂ treatments, but soluble carbohydrate and alpha-cellulose concentrations were higher, and percentage lignin lower, in the elevated CO₂ treatments. The tent treatments significantly retarded shoot decomposition in both ecosystems, probably because of lower litter bag moisture contents, although the additional precipitation treatment had no effect on mass loss from the above-ground material. The results suggest that neither additional summer precipitation (up to 58%), nor soil temperature increase of 1 degrees C, which may occur by the end of the next century as an effect of a predicted 4 degrees C rise in air temperature, had an appreciable effect on root decomposition in the short term in a high Arctic soil. However, at the low Arctic site, greater root decomposition, and a lower pool of root N remaining, were observed where soil temperature was increased by 2 degrees C in response to a 4 degrees C rise in air temperature. These results suggest that decomposition below-ground in this ecosystem would increase as an effect of predicted climate change. These data also show that there is a difference in the initial results of decomposition processes between the two Arctic ecosystems in response to simulated environmental change.

KEYWORDS: CARBON DIOXIDE, CLIMATE CHANGE, FOREST, GRASS, LEAF LITTER, MINERALIZATION, NITROGEN, QUALITY, SOILS, TUNDRA

2010

Robinson, D., and J.P. Conroy. 1999. A possible plant-mediated feedback between elevated CO₂, denitrification and the enhanced greenhouse effect. *Soil Biology and Biochemistry* 31(1):43-53.

Natural abundances (δ) of N-15 were used to detect effects of elevated atmospheric CO₂ concentration ([CO₂]) and soil wetness on soil N transformations in the presence or absence of plants. An elevated [CO₂] of 1000 μ mol L⁻¹ reduced water use by the perennial C-4 grass *Panicum coloratum* and stimulated root and whole-plant growth. Soil remained wetter between infrequent irrigations than in soil supporting *P. coloratum* grown in an ambient [CO₂] (350 μ mol L⁻¹). The $\delta(15)$ N value of soil nitrate increased from -2.4 to +9.6 parts per thousand as nitrate was depleted from the soil, but remained unchanged in unplanted soil. The change in $\delta(15)$ N of soil nitrate was greatest in frequently watered soil regardless of [CO₂], and in infrequently watered soil only in elevated [CO₂]. It was least in the infrequently watered, ambient [CO₂] treatment. Isotope mass balances and N-15/N-14 fractionation theory identified denitrification as the most probable cause of this effect, through the effect of elevated [CO₂] on soil wetness. Nitrification, nitrogen assimilation, leaching or ammonia volatilisation were unlikely causes. The data suggest a positive, plant-induced effect of elevated atmospheric [CO₂] on denitrification. The possibility exists, therefore, for a positive feedback between elevated atmospheric [CO₂], a greater soil-to-atmosphere N₂O flux and an exacerbation of the enhanced greenhouse effect. (C) 1998 Elsevier Science Ltd. All rights reserved.

KEYWORDS: ATMOSPHERIC CO₂, CARBON-DIOXIDE ENRICHMENT, GRASSLAND, ISOTOPE FRACTIONATION, N-15, NATURAL ABUNDANCE, NITRIFICATION, NITROGEN, SOIL, WATER-USE

2011

Robinson, M.F., J. Heath, and T.A. Mansfield. 1998. Disturbances in stomatal behaviour caused by air pollutants. *Journal of Experimental Botany* 49:461-469.

Many atmospheric pollutants, even when present at relatively low concentrations, may interfere with the control of stomatal aperture, and they thus have the potential to upset the water balance of the leaf or the whole plant. Although at high concentrations pollutants such as SO₂ and O₃ usually cause stomatal closure, at low concentrations stomatal conductance is often increased. As well as creating a risk of loss of control of water relations, this is likely to increase the dose of the pollutant entering the mesophyll. It is, however, difficult to generalize about the nature of the physiological disturbances caused by pollutants because of variation in the responses between plants. In some cases the effects may be peculiar to one, or just a few, species. Two mechanisms underlying the interference with stomatal control have recently been identified, one involving O₃ and the other CO₂. In *Aster tripolium* (sea aster) stomata in detached epidermal strips close as the external Na⁺ concentration is increased, and it has been proposed that this phenomenon is involved in the regulation of salt loading of shoot tissues. Ozone has been shown to have the capacity to interfere with Na⁺-induced stomatal closure, and the possibility that it therefore disrupts an aspect of salinity tolerance in this species is worthy of further research. Elevated CO₂, on the other hand, has been found to interfere with the control of water relations of beech (*Fagus sylvatica*): for a given degree of drought, stomatal conductance and rates of soil water depletion were significantly higher in elevated CO₂ than in ambient air. It is normally assumed that atmospheric CO₂-enrichment will lead to increased plant productivity and improved water economy, while also providing some protection against other atmospheric pollutants through partial stomatal closure. However, the response of beech indicates that in some species there may also be detrimental effects of CO₂-enrichment on plant-water relations.

KEYWORDS: *ABIES L. KARST, ABSCISIC-ACID, ASTER-TRIPOLIUM L., CARBON DIOXIDE, CYTOSOLIC-FREE CALCIUM, GUARD-CELLS, PLANTAGO-MAJOR L., PLASMA-MEMBRANE, SULFUR-DIOXIDE, VICIA-FABA L.*

2012

Rocheffort, L., and F.A. Bazzaz. 1992. Growth-response to elevated CO₂ in seedlings of 4 cooccurring birch species. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 22(11):1583-1587.

Seedlings of four birch species were examined to evaluate the presence and extent of phylogenetic constraints on the response of species to global CO₂ change. The species differ in their habitat preferences and their successional status. Seedlings were grown for 3 months at near ambient (380 µL L⁻¹) and double (690 µL L⁻¹) CO₂ concentrations in glasshouses. We found the following: (i) yellow birch (*Betula alleghaniensis* Britton) was the only species whose survival differed among CO₂ treatments. Survival was slightly increased by elevated CO₂. (ii) All growth parameters considered in all four species were significantly stimulated by enriched CO₂ Conditions, but the magnitude of response was different among species. The most shade-intolerant, fast-growing species (grey birch; *Betula populifolia* Marsh.) took greater advantage of the elevated CO₂ resource than the more shade-tolerant, later successional species (e.g., yellow birch). (iii) Patterns of allocation, shoot architecture, and leaf nitrogen content were affected differently by CO₂ concentrations for the different species. (iv) The presence and identity of a neighbor did not influence the magnitude or pattern of response to CO₂ in birches of a given community. Our results suggest that congeneric species might be more similar in their response to global CO₂ in comparison to unrelated species of the same ecosystem that had been studied by others, despite the fact that these closely related birch

species differ in their habitat preferences and successional status.

KEYWORDS: *ENRICHMENT, FOREST, LIQUIDAMBAR-STYRACIFLUA, NITROGEN, PINUS-TAEDA SEEDLINGS, PLANT, TREES*

2013

Roden, J.S., and M.C. Ball. 1996. The effect of elevated [CO₂] on growth and photosynthesis of two eucalyptus species exposed to high temperatures and water deficits. *Plant Physiology* 111(3):909-919.

Two species of eucalyptus (*Eucalyptus macrorhyncha* and *Eucalyptus rossii*) were grown for 8 weeks in either ambient (350 µL L⁻¹) or elevated (700 µL L⁻¹) CO₂ concentrations, either well watered or without water additions, and subjected to a daily, 3-h high-temperature (45 degrees C, maximum) and high-light (1250 µmol photons m⁻² s⁻¹), maximum stress period. Water-stressed seedlings of *E. macrorhyncha* had higher leaf water potentials when grown in elevated [CO₂]. Growth analysis indicated that increased [CO₂] may allow eucalyptus species to perform better during conditions of low soil moisture. A down-regulation of photosynthetic capacity was observed for seedlings grown in elevated [CO₂] when well watered but not when water stressed. Well-watered seedlings grown in elevated [CO₂] had lower quantum efficiencies as measured by chlorophyll fluorescence (the ratio of variable to maximal chlorophyll fluorescence [F_v/F_m]) than seedlings grown in ambient [CO₂] during the high-temperature stress period. However, no significant differences in F_v/F_m were observed between CO₂ treatments when water was withheld. The reductions in dark-adapted F_v/F_m for plants grown in elevated [CO₂] were not well correlated with increased xanthophyll cycle photoprotection. However, reductions in the F_v/F_m were correlated with increased levels of nonstructural carbohydrates. The reduction in quantum efficiencies for plants grown in elevated [CO₂] is discussed in the context of feedback inhibition of electron transport associated with starch accumulation and variation in sink strength.

KEYWORDS: *ATMOSPHERIC CO2, CARBON DIOXIDE, CHLOROPHYLL FLUORESCENCE, DROUGHT, ELECTRON-TRANSPORT, LEAVES, LIGHT, PHOTOSYSTEM, SEEDLINGS, STRESS*

2014

Roden, J.S., and M.C. Ball. 1996. Growth and photosynthesis of two eucalypt species during high temperature stress under ambient and elevated [CO₂]. *Global Change Biology* 2(2):115-128.

Two species of eucalypt (*Eucalyptus macrorhyncha* and *E. rossii*) were grown under conditions of high temperatures (45 degrees C, maximum) and high light (1500 µmol m⁻² s⁻¹, maximum) at either ambient (350 µL L⁻¹) or elevated (700 µL L⁻¹) CO₂ concentrations for 8 weeks. The growth enhancement, in terms of total dry weight, was 41% and 103% for *E. macrorhyncha* and *E. rossii*, respectively, when grown in elevated [CO₂]. A reduction in specific leaf area and increased concentrations of non-structural carbohydrates were observed for leaves grown in elevated [CO₂]. Plants grown in elevated [CO₂] had an overall increase in photosynthetic CO₂ assimilation rate of 27%; however, when measured at the same CO₂ concentration a down-regulation of photosynthesis was evident especially for *E. macrorhyncha*. During the midday period when temperatures and irradiances were maximal, photosynthetic efficiency as measured by chlorophyll fluorescence (F_v/F_m) was lower in *E. macrorhyncha* than in *E. rossii*. Furthermore, F_v/F_m was lower in leaves of *E. macrorhyncha* grown under elevated than under ambient [CO]. These reductions in F_v/F_m were accompanied by increases in both photochemical (q(p)) and nonphotochemical quenching (q(N) and NPQ), and by increases in the concentrations of xanthophyll cycle pigments with an increased

proportion of the total xanthophyll cycle pool comprising of antheraxanthin and zeaxanthin. Thus, increased atmospheric [CO₂] may enhance photoinhibition when environmental stresses such as high temperatures limit the capacity of a plant to respond with growth to elevated [CO₂].

KEYWORDS: CARBON DIOXIDE, CHLOROPHYLL FLUORESCENCE, COTTON PLANTS, ELECTRON-TRANSPORT, LIGHT, MECHANISM, PHOTOINHIBITION, QUANTUM YIELD, RESPONSES, SEEDLINGS

2015

Roden, J.S., J.J.G. Egerton, and M.C. Ball. 1999. Effect of elevated [CO₂] on photosynthesis and growth of snow gum (*Eucalyptus pauciflora*) seedlings during winter and spring. *Australian Journal of Plant Physiology* 26(1):37-46.

Snow gum (*Eucalyptus pauciflora* Sieb. ex Spreng.) seedlings were grown from autumn through spring in open top chambers located in a pasture naturally subject to freezing temperatures in either ambient or elevated (350 μ L L⁻¹ above ambient) CO₂ concentrations. Sustained reduction in quantum efficiency, as measured by chlorophyll fluorescence (F-v/F-m), in over-wintering leaves may be related to seasonal down-regulation of photosynthesis, combined with cumulative effects of freeze-induced damage to the photosynthetic apparatus, with the effect being greater in leaves grown under elevated [CO₂]. Down-regulation of photosynthesis apparently occurred in response to seasonal limitations to growth which were not overcome by elevation of [CO₂] despite temperatures being favorable for photosynthesis during most of the photoperiod. Elevated [CO₂] had no effect on growth of over-wintering seedlings, but enhanced growth in spring when minimum temperatures rose consistently above freezing. As there were no effects of elevated [CO₂] on allocation, the stimulation of growth in spring was attributable to increase in net assimilation rates. Thus seasonal differences in photoinhibition were consistent with seasonal differences in the capacity for growth, with plants grown under elevated [CO₂] having to dissipate more excess excitation energy over-winter.

KEYWORDS: CHLOROPHYLL FLUORESCENCE, CLIMATE, COLD-INDUCED PHOTOINHIBITION, ELECTRON-TRANSPORT, LEAVES, LOW-TEMPERATURE, PERFORMANCE, QUANTUM YIELD, SCOTS PINE, WATER-STRESS

2016

Roden, J.S., D.J. Wiggins, and M.C. Ball. 1997. Photosynthesis and growth of two rain forest species in simulated gaps under elevated CO₂. *Ecology* 78(2):385-393.

Two species common to the temperate rain forests of New South Wales, Australia (*Doryphora sassafras* and *Acmena smithii*) were grown for 2 wk in either ambient (350 μ L/L) or elevated (700 μ L/L) CO₂ concentrations and low light (30 μ mol photons \cdot m⁻² \cdot s⁻¹) after which the seedlings were exposed for over 9 wk to a midday 2-h highlight period (1250 μ mol photons \cdot m⁻² \cdot s⁻¹, maximum) to simulate a tree fall gap. For both species, plants grown in elevated CO₂ had greater biomass than plants grown in ambient CO₂. However, relative increases in biomass were greater in *Acmena*, which is an early-successional species, than *Doryphora*, which is a late-successional species. *Doryphora sassafras* also had greater reductions in photosynthetic efficiency, as measured by chlorophyll fluorescence techniques (F-v/F-m) upon exposure to the high-light treatment than *Acmena*. Recovery in quantum efficiencies over time was observed for *Doryphora*, implying physiological acclimation to the new light environment. Plants grown in elevated CO₂ had lower values of F-v/F-m than plants grown in ambient CO₂, but these differences between CO₂ treatments were only significant for the late-successional *Doryphora*.

Although exposure to the simulated tree fall gap dramatically increased the conversion of pigments of the xanthophyll cycle, as well as increased the total pool size of xanthophyll cycle pigments relative to total chlorophyll concentration, there were no differences in either parameter between CO₂ treatments. Leaves of *Doryphora* and those seedlings grown in elevated CO₂ had greater starch concentrations than *Acmena* and those seedlings grown in ambient CO₂, respectively. The reduction in quantum efficiencies for plants grown in elevated CO₂ and exposed to a simulated tree fall gap is discussed in the context of the importance of gap phase regeneration for species in rain forest ecosystems and the potential effects of global change on those processes.

KEYWORDS: ACCLIMATION, ALOCASIA-MACRORRHIZA, DIVERSITY, ELECTRON-TRANSPORT, LIGHT, PHOTOINHIBITION, RESPONSES, SEEDLINGS, TOLERANT, TREES

2017

Roderick, M.L., S.L. Berry, and I.R. Noble. 1999. The relationship between leaf composition and morphology at elevated CO₂ concentrations. *New Phytologist* 143(1):63-72.

The composition and morphology of leaves exposed to elevated [CO₂] usually change so that the leaf nitrogen (N) per unit dry mass decreases and the leaf dry mass per unit area increases. However, at ambient [CO₂], leaves with a high leaf dry mass per unit area usually have low leaf N per unit dry mass. Whether the changes in leaf properties induced by elevated [CO₂] follow the same overall pattern as that at ambient [CO₂] has not previously been addressed. Here we address this issue by using leaf measurements made at ambient [CO₂] to develop an empirical model of the composition and morphology of leaves. Predictions from that model are then compared with a global database of leaf measurements made at ambient [CO₂]. Those predictions are also compared with measurements showing the impact of elevated [CO₂]. In the empirical model both the leaf dry mass and liquid mass per unit area are positively correlated with leaf thickness, whereas the mass of C per unit dry mass and the mass of N per unit liquid mass are constant. Consequently, both the N:C ratio and the surface area:volume ratio of leaves are positively correlated with the liquid content. Predictions from that model were consistent with measurements of leaf properties made at ambient [CO₂] from around the world. The changes induced by elevated [CO₂] follow the same overall trajectory. It is concluded that elevated [CO₂] enhances the rate at which dry matter is accumulated but the overall trajectory of leaf development is conserved.

KEYWORDS: ATMOSPHERIC CO₂, CARBON DIOXIDE, GRADIENT, GROWTH, INSECT HERBIVORY, LEAVES, NITROGEN, PHOTOSYNTHETIC CAPACITY, RAIN-FOREST, RESPONSES

2018

Rodriguez, D., M. Van Oijen, and A.H.M.C. Schapendonk. 1999. LINGRA-CC: a sink-source model to simulate the impact of climate change and management on grassland productivity. *New Phytologist* 144(2):359-368.

A simulation model for the prediction of grassland (*Lolium perenne*) productivity under conditions of climate change is described and validated for grass growing in the Wageningen Rhizolab, Wageningen, The Netherlands. In this work the model was used to study the impact of different management strategies on the productivity of grassland under present and increased atmospheric CO₂ concentrations. In LINGRA-CC simulated key processes are light utilization, leaf formation, leaf elongation, tillering and carbon partitioning. The daily growth rate is determined by the minimum of a sink and a source term. As in a previous model (LINGRA), the potential growth of the sink depends on the mean daily temperature, and can be modified by the effects of the availability of assimilates on tillering. The growth of roots is calculated

from the amount of carbohydrates the shoot is unable to utilize when the number or activity of the sinks is small (overflow hypothesis). The main difference between LINGRA and LINGRA-CC is the way the source of assimilates for growth is calculated. Assimilate production depends on intercepted radiation, and a photosynthetic light-use efficiency (LUE) calculated as a function of CO₂, temperature, light intensity and the Rubisco concentration of upper leaves. Other differences are that in LINGRA-CC, the specific shoot area for new growth depends on the level of reserves. Data from two independent experiments with *L. perenne* swards, grown in enclosures at two levels of CO₂ during 1994 and 1995, were used to calibrate and validate the model, respectively. The model predicted well the observed amounts of harvested biomass, and the dynamics of the leaf area index, tiller number and specific shoot area. LINGRA-CC was used to study the effects of different combinations of cutting interval and cutting height on biomass production, at ambient (350 $\mu\text{mol mol}^{-1}$ CO₂) and double (700 $\mu\text{mol mol}^{-1}$ CO₂) CO₂ conditions. Under both ambient and doubled CO₂, maximum biomass was produced with cuttings of leaf area index >1, and at cutting intervals of 20 and 17 d for ambient and increased CO₂ environments, respectively. Under high CO₂ conditions the curling interval for maximum yield was 15% shorter than at ambient CO₂. However, the gain in harvested biomass obtained by reducing the cutting interval by 3 d under high CO₂ conditions was negligible.

KEYWORDS: ELEVATED CO₂, GROWTH, INCREASED CO₂ CONCENTRATION, *LOLIUM-PERENNE*, PHOTOSYNTHESIS, PRAIRIE GRASS, RYEGRASS, TEMPERATURE, USE EFFICIENCY, WHEAT

2019

Rogers, A., B.U. Fischer, J. Bryant, M. Frehner, H. Blum, C.A. Raines, and S.P. Long. 1998. Acclimation of photosynthesis to elevated CO₂ under low-nitrogen nutrition is affected by the capacity for assimilate utilization. Perennial ryegrass under free-air CO₂ enrichment. *Plant Physiology* 118(2):683-689.

Acclimation of photosynthesis to elevated CO₂ has previously been shown to be more pronounced when N supply is poor. Is this a direct effect of N or an indirect effect of N by limiting the development of sinks for photoassimilate? This question was tested by growing a perennial ryegrass (*Lolium perenne*) in the field under elevated (60 Pa) and current (36 Pa) partial pressures of CO₂ (pCO₂) at low and high levels of N fertilization. Cutting of this herbage crop at 4- to 8-week intervals removed about 80% of the canopy, therefore decreasing the ratio of photosynthetic area to sinks for photoassimilate. Leaf photosynthesis, *in vivo* carboxylation capacity, carbohydrate, N, ribulose-1,5-bisphosphate carboxylase/oxygenase, sedoheptulose-1,7-bisphosphatase, and chloroplastic fructose-1,6-bisphosphatase levels were determined for mature lamina during two consecutive summers, just before the cut, when the canopy was relatively large, growth at elevated pCO₂ and low N resulted in significant decreases in carboxylation capacity and the amount of ribulose-1,5-bisphosphate carboxylase/oxygenase protein. In high N there were no significant decreases in carboxylation capacity or proteins, but chloroplastic fructose-1,6-bisphosphatase protein levels increased significantly. Elevated pCO₂ resulted in a marked and significant increase in leaf carbohydrate content at low N, but had no effect at high N. This acclimation at low N was absent after the harvest, when the canopy size was small. These results suggest that acclimation under low N is caused by limitation of sink development rather than being a direct effect of N supply on photosynthesis.

KEYWORDS: ACCUMULATION, CARBON DIOXIDE, GAS-EXCHANGE, GROWTH, LEAVES, PLANTS, RISING ATMOSPHERIC CO₂, SOURCE-SINK RELATIONS, TRANSCRIPT LEVELS, *TRIFOLIUM-REPENS* L

2020

Rogers, G.S., P.W. Gras, I.L. Batey, P.J. Milham, L. Payne, and J.P. Conroy. 1998. The influence of atmospheric CO₂ concentration on the protein, starch and mixing properties of wheat flour. *Australian Journal of Plant Physiology* 25(3):387-393.

Wheat (*Triticum aestivum* L.) cultivars Hartog and Rosella were grown at CO₂ concentrations of 280 $\mu\text{mol L}^{-1}$ (representing the pre-industrial CO₂ concentration), 350 $\mu\text{mol L}^{-1}$ (ambient) and 900 $\mu\text{mol L}^{-1}$ (an extreme projection of atmospheric CO₂ concentration). The plants were grown in naturally lit glasshouses in 7 L pots containing soil to which basal nutrients had been added and the pH adjusted to 6.5. Hartog yielded 2.4 g of grain per plant when grown at 280 $\mu\text{mol L}^{-1}$ CO₂. This yield was increased by 38% and 75% at CO₂ concentrations of 350 $\mu\text{mol L}^{-1}$ and 900 $\mu\text{mol L}^{-1}$ respectively. These changes were due to increases in both grain number and individual grain weight as the level of CO₂ was raised. The yield of Rosella was unaffected by altering the CO₂ concentration. Increasing the CO₂ concentration reduced grain protein concentration of cv. Hartog from 17.4% at 280 $\mu\text{mol L}^{-1}$ CO₂ to 16.5% and 16% at CO₂ concentrations of 350 $\mu\text{mol L}^{-1}$ and 900 $\mu\text{mol L}^{-1}$ respectively. The grain protein concentration of cv. Rosella was reduced from 10.7% to 10.2% by increasing the CO₂ concentration from 280 $\mu\text{mol L}^{-1}$ to 350 $\mu\text{mol L}^{-1}$; however, an additional increase in the CO₂ concentration to 900 $\mu\text{mol L}^{-1}$ had no effect on grain protein concentration. In Hartog flour, the highest proportion of polymeric protein in the flour (7.7%) occurred at 280 $\mu\text{mol L}^{-1}$ CO₂. This was reduced to 6.3% at 350 $\mu\text{mol L}^{-1}$ CO₂ but then increased again to 7.0% at 900 $\mu\text{mol L}^{-1}$ CO₂. These changes in concentration of polymeric protein were correlated ($r^2=0.58$) with changes in mixing properties. The mixing time required to produce optimum dough strength was greatest at 900 $\mu\text{mol L}^{-1}$ CO₂ (181 s), then 141 s and 151 s at 350 $\mu\text{mol L}^{-1}$ CO₂ and 280 $\mu\text{mol L}^{-1}$ CO₂ respectively. These changes in mixing time could not be explained by changes in grain protein concentration. The proportion of 'B' starch granules (<10 μm diameter) increased from 25% of total weight of starch at 280 $\mu\text{mol L}^{-1}$ CO₂ to 30% at CO₂ concentrations 350 and 900 $\mu\text{mol L}^{-1}$. There were generally no effects of CO₂ concentration on dough mixing properties or starch granule size distribution for Rosella.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO₂, GENOTYPES, GRAIN QUALITY, NITROGEN, NUTRITION, STRESS, TEMPERATURE, WINTER-WHEAT, YIELD

2021

Rogers, G.S., P.J. Milham, M. Gillings, and J.P. Conroy. 1996. Sink strength may be the key to growth and nitrogen responses in N-deficient wheat at elevated CO₂. *Australian Journal of Plant Physiology* 23(3):253-264.

The influence of elevated CO₂ (350, 550 and 900 $\mu\text{mol L}^{-1}$) and N supplies ranging from deficient to excess (0-133 mg N kg⁻¹ soil week⁻¹) on the leaf N concentration and shoot growth of wheat (*Triticum aestivum* L.), cultivar Hartog, was investigated. Shoot growth was 30% greater at 550 $\mu\text{mol L}^{-1}$ compared to ambient CO₂ at all levels of N supply. When the CO₂ concentration was increased to 900 $\mu\text{mol L}^{-1}$, there was no increase in shoot growth at low N supply but it more than doubled at high N supply (67 mg N kg⁻¹ soil week⁻¹). Growth effects were closely matched by changes in sink development, suggesting that sink strength, mediated through N supply controlled the shoot growth response to elevated CO₂. The shoot N concentration was lower at each level of CO₂ enrichment and the greatest effect (30% reduction) occurred at 900 $\mu\text{mol L}^{-1}$ CO₂, 33 mg N kg⁻¹ soil week⁻¹. The effect of high CO₂ on shoot N concentration diminished as N supply increased and, at the highest N addition rate, there was only a 7% reduction. Changes in foliar N concentration due to CO₂ enrichment were closely correlated with lower soluble protein concentration, accounting for 58% of the total leaf N reduction. Ribulose-1,5-

bisphosphate carboxylase/oxygenase (Rubisco) levels were also reduced at high CO₂ and N was allocated away from Rubisco and into other soluble proteins at high CO₂ when N supply was low. Nonstructural carbohydrate concentration (dry weight basis) was greatest at 900 µmol CO₂ L⁻¹ and low N supply and may have reduced Rubisco concentration via a feed-back response. Critical foliar N concentrations (N concentration at 90 % of maximum shoot growth) were reduced from 43 mg g⁻¹ at ambient CO₂ to 39 and 38 mg g⁻¹ at 550 and 900 µmol CO₂ L⁻¹, respectively. Elevated CO₂, at N supplies of 0-17 mg N kg⁻¹ soil week⁻¹, reduced flour protein concentration by 9-13 %.

KEYWORDS: CARBAMYLATION, CARBON DIOXIDE, ENRICHMENT, NUTRITION, PHOTOSYNTHESIS, PLANTS, PROTEIN, RIBULOSE-1,5-BISPHOSPHATE CARBOXYLASE, STRESS, TOBACCO

2022

Rogers, G.S., P.J. Milham, M.C. Thibaud, and J.P. Conroy. 1996. Interactions between rising CO₂ concentration and nitrogen supply in cotton .1. Growth and leaf nitrogen concentration. *Australian Journal of Plant Physiology* 23(2):119-125.

The influence of sink development on the response of shoot growth in cotton (*Gossypium hirsutum* L. cv. Siokra BT1-4) was investigated by growing plants at three levels of CO₂ concentration: 350 (ambient), 550 and 900 µmol L⁻¹ and six levels of nitrogen (N) supply ranging from deficient to excess (0-133 mg N kg⁻¹ soil week⁻¹). Changes in leaf N concentration were also investigated. At 59 days after sowing, there was an average 63% increase in shoot growth at 550 µmol CO₂ L⁻¹ compared with ambient CO₂-grown plants, with no significant growth increase at 900 µmol CO₂ L⁻¹ and, this response was closely matched by sink development (flower number and stem weight). Low N supply restricted the responses of both sink development and shoot growth to high CO₂. At elevated CO₂, leaf N concentration was reduced by an average 27% at low to adequate N supply. The high CO₂-induced reduction in leaf N concentration, however, disappeared when the N supply was increased to a high level of 133 mg N kg⁻¹ soil week⁻¹. These CO₂ effects on leaf N concentration were smaller when N was expressed per unit leaf area, apparently due to a combination of the effects of elevated CO₂ or high N supply reducing specific leaf area and, to an N uptake limitation at low to moderate levels of N supply. The critical foliar N concentrations (leaf N concentration at 90% of maximum shoot growth) were reduced from 42 to 38 and 36 mg g⁻¹ when CO₂ concentrations were increased from 350 to 550 and 900 µmol L⁻¹ respectively, indicating that changes in fertiliser management may be required under changing CO₂ concentrations.

KEYWORDS: C-3 PLANTS, CARBOHYDRATE, CARBON, LEAVES, PHOTOSYNTHESIS, WHEAT

2023

Rogers, G.S., L. Payne, P. Milham, and J. Conroy. 1993. Nitrogen and phosphorus requirements of cotton and wheat under changing atmospheric CO₂ concentrations. *Plant and Soil* 156:231-234.

The influence of increasing atmospheric CO₂ on shoot growth, leaf nitrogen and phosphorus concentrations and carbohydrate composition was investigated in cotton and wheat. Shoot dry weight of both species was generally higher at elevated CO₂, especially at high rates of available soil N and P. Critical leaf N concentration was reduced but critical P concentration was increased in both species at high CO₂.

KEYWORDS: CARBOHYDRATE, ENRICHMENT, GROWTH, METABOLISM, STRESS

2024

Rogers, H.H., and R.C. Dahlman. 1993. Crop responses to CO₂ enrichment. *Vegetatio* 104:117-131.

Carbon dioxide is rising in the global atmosphere, and this increase can be expected to continue into the foreseeable future. This compound is an essential input to plant life. Crop function is affected across all scales from biochemical to agro-ecosystem. An array of methods (leaf cuvettes, field chambers, free-air release systems) are available for experimental studies of CO₂ effects. Carbon dioxide enrichment of the air in which crops grow usually stimulates their growth and yield. Plant structure and physiology are markedly altered. Interactions between CO₂ and environmental factors that influence plants are known to occur. Implications for crop growth and yield are enormous. Strategies designed to assure future global food security must include a consideration of crop responses to elevated atmospheric CO₂. Future research should include these targets: search for new insights, development of new techniques, construction of better simulation models, investigation of belowground processes, study of interactions, and the elimination of major discrepancies in the scientific knowledge base.

KEYWORDS: AGRICULTURAL PRODUCTIVITY, AIR-TEMPERATURE, CLIMATIC CHANGE, ELEVATED CARBON-DIOXIDE, INCREASING ATMOSPHERIC CO₂, MINERAL NUTRITION, PLANT GROWTH, SOYBEAN CANOPY, WATER-USE EFFICIENCY, WINTER-WHEAT

2025

Rogers, H.H., C.M. Peterson, J.N. McCrimmon, and J.D. Cure. 1992. Response of plant-roots to elevated atmospheric carbon-dioxide. *Plant, Cell and Environment* 15(6):749-752.

Plant root response to atmospheric CO₂ enrichment can be great. Results from this controlled environment investigation demonstrate substantial effects on root system architecture, micromorphology and physiology. The most pronounced effects were an increase in root length (110%) and root dry weight (143%). Root diameter, stele diameter, cortex width, root/shoot and root weight ratios all increased; root numbers did not increase. The long-term implications for belowground processes could be enormous.

KEYWORDS: GROWTH

2026

Rogers, H.H., S.A. Prior, and E.G. O'Neill. 1992. Cotton root and rhizosphere responses to free-air CO₂ enrichment. *Critical Reviews in Plant Sciences* 11(2-3):251-263.

KEYWORDS: AGRICULTURE, CARBON DIOXIDE, CO₂, GROWTH, INFECTION, SOIL, WHEAT, YIELD

2027

Rogers, H.H., S.A. Prior, and G.B. Runion. 1993. Effects of elevated atmospheric CO₂ on soybean and sorghum root-growth. *Plant Physiology* 102(1):173.

2028

Rogers, H.H., S.A. Prior, G.B. Runion, and R.J. Mitchell. 1996. Root to shoot ratio of crops as influenced by CO₂. *Plant and Soil* 187(2):229-248.

Crops of tomorrow are likely to grow under higher levels of atmospheric CO₂. Fundamental crop growth processes will be affected and chief

among these is carbon allocation. The root to shoot ratio (R:S, defined as dry weight of root biomass divided by dry weight of shoot biomass) depends upon the partitioning of photosynthate which may be influenced by environmental stimuli. Exposure of plant canopies to high CO₂ concentration often stimulates the growth of both shoot and root, but the question remains whether elevated atmospheric CO₂ concentration will affect roots and shoots of crop plants proportionally. Since elevated CO₂ can induce changes in plant structure and function, there may be differences in allocation between root and shoot, at least under some conditions. The effect of elevated atmospheric CO₂ on carbon allocation has yet to be fully elucidated, especially in the context of changing resource availability. Herein we review root to shoot allocation as affected by increased concentrations of atmospheric CO₂ and provide recommendations for further research. Review of the available literature shows substantial variation in R:S response for crop plants. In many cases (59.5%) R:S increased, in a very few (3.0%) remained unchanged, and in others (37.5%) decreased. The explanation for these differences probably resides in crop type, resource supply, and other experimental factors. Efforts to understand allocation under CO₂ enrichment will add substantially to the global change response data base.

KEYWORDS: ATMOSPHERIC PARTIAL-PRESSURE, CARBOHYDRATE CONTENT, CARBON-DIOXIDE ENRICHMENT, DRY-MATTER, ELEVATED CO₂, MECHANICAL IMPEDANCE, PHOTOSYNTHETIC ACCLIMATION, PLANT GROWTH, WATER-STRESS, YIELD RESPONSES

2029

Rogers, H.H., G.B. Runion, and S.V. Krupa. 1994. Plant-responses to atmospheric CO₂ enrichment with emphasis on roots and the rhizosphere. *Environmental Pollution* 83(1-2):155-189.

Empirical records provide incontestable evidence of global changes; foremost among these changes is the rising concentration of CO₂ in the earth's atmosphere. Plant growth is nearly always stimulated by elevation of CO₂. Photosynthesis increases, more plant biomass accumulates per unit of water consumed, and economic yield is enhanced. The profitable use of supplemental CO₂ over years of greenhouse practice points to the value of CO₂ for plant production. Plant responses to CO₂ are known to interact with other environmental factors, e.g. light, temperature, soil water, and humidity. Important stresses including drought, temperature, salinity, and air pollution have been shown to be ameliorated when CO₂ levels are elevated. In the agricultural context, the growing season has been shortened for some crops with the application of more CO₂; less water use has generally, but not always, been observed and is under further study; experimental studies have shown that economic yield for most crops increases by about 33% for a doubling of ambient CO₂ concentration. However, there are some reports of negligible or negative effects. Plant species respond differently to CO₂ enrichment, therefore, clearly competitive shifts within natural communities could occur. Though of less importance in managed agro-ecosystems, competition between crops and weeds could also be altered. Tissue composition can vary as CO₂ increases (e.g. higher C:N ratios) leading to changes in herbivory, but tests of crop products (consumed by man) from elevated CO₂ experiments have generally not revealed significant differences in their quality. However, any CO₂-induced change in plant chemical or structural make-up could lead to alterations in the plant's interaction with any number of environmental factors- physicochemical or biological. Host-pathogen relationships, defense against physical stressors, and the capacity to overcome resource shortages could be impacted by rises in CO₂. Root biomass is known to increase but, with few exceptions, detailed studies of root growth and function are lacking. Potential enhancement of root growth could translate into greater rhizodeposition, which, in turn, could lead to shifts in the rhizosphere itself. Some of the direct effects of CO₂ on vegetation have been reasonably well-studied, but for others work has been inadequate. Among these neglected areas are plant roots and the rhizosphere.

Therefore, experiments on root and rhizosphere response in plants grown in CO₂-enriched atmospheres will be reviewed and, where possible, collectively integrated. To this will be added data which have recently been collected by us. Having looked at the available data base, we will offer a series of hypotheses which we consider as priority targets for future research.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, ELEVATED CO₂, FIELD-GROWN SOYBEANS, KUDZU PUERARIA-LOBATA, LONG-TERM EXPOSURE, OPEN-TOP CHAMBERS, PINUS-TAEDA SEEDLINGS, SOUR ORANGE TREES, SOYBEAN GLYCINE-MAX, WATER-USE EFFICIENCY

2030

Rolland, C., V. Petitcolas, and R. Michalet. 1998. Changes in radial tree growth for *Picea abies*, *Larix decidua*, *Pinus cembra* and *Pinus uncinata* near the alpine timberline since 1750. *Trees-Structure and Function* 13(1):40-53.

Changes in radial growth of the four coniferous species growing in the French Alps near the upper treeline are investigated. Thirty-seven populations of Norway spruce [*Picea abies* (L.) Karst.], European larch (*Larix decidua* Mill.), Swiss stone pine (*Pinus cembra* L.) and mountain pine (*Pinus uncinata* Mill. ex Mirb.) were sampled by taking 1320 cores and analysing tree-ring widths. Sites were chosen in various climatic conditions (macroclimate and aspect) and on two kinds of bedrock in order to take into account the ecological behaviour of these species. Belledonne, Moyenne-Tarentaise: Haute-Maurienne and Briançonnais areas were sampled along increasing gradients of summer aridity and winter continentality. The calculation of time series after removing the age trend brings strong evidence for an increase in radial growth during the two last centuries, but with different stages and fluctuations for each species. This growth trend is significantly enhanced since 1860 for the spruce, and since 1920 for the two pine species. Furthermore, it also appears on *Larix decidua* with the same pattern despite periodical growth reduction due to attacks of the larch bud moth (*Zeiraphera diniana* Gn.). The analysis of ring-widths at a given cambial age reveals that this enhanced phenomenon is observed especially during the tree's early years (25-75 years). The analysis of four regional climatic series, and three longer series of temperature (in farther single sites) reveals synchronous decadal fluctuations and an evident secular increase in minimum temperatures (especially in January and from July to October), that may be involved in tree-growth enhancement. Thermic amplitudes are significantly reduced during the whole growing period, what is more pronounced in Belledonne, the most oceanic region. Long term growth changes are well described by stepwise regression models, especially for the pine species. These models involved both a linear trend (CO₂ concentration or N-deposition) and low frequency of Turin monthly temperatures. However, they show different patterns than those observed from response functions at a yearly scale.

KEYWORDS: CARBON DIOXIDE, CO₂, FOREST, FRANCE, HIGH-ELEVATION SITES, RESPONSES, SPRUCE MODEL-ECOSYSTEMS, TEMPERATURE, TRENDS

2031

Ronen-Tarazi, M., D.J. Bonfil, D. Schatz, and A. Kaplan. 1998. Cyanobacterial mutants impaired in bicarbonate uptake isolated with the aid of an inactivation library. *Canadian Journal of Botany-Revue Canadienne De Botanique* 76(6):942-948.

An inactivation library consisting of genomic fragments ligated within a modified bluescript vector was used to isolate several new high CO₂ requiring mutants of *Synechococcus* PCC7942. The mutants described here were impaired in the ability to accumulate C₄ internally when supplied with HCO₃⁻. The relevant genomic regions bearing novel genes

involved in the ability to transport and to accumulate Ci within the cells and thus to grow under low-CO₂ conditions are presented. Some of the mutants were also impaired in ability to adjust to an elevated pH in their medium. We show that the use of inactivation libraries enabled cloning of genes encoding membrane-located proteins; we point to mutations introduced by the single cross-recombination events resulting in the formation of some of these mutants. Possible artifacts that may result in incorrect identification of genes, the inactivation of which could have led to the observed phenotype, are discussed.

KEYWORDS: CO₂ CONCENTRATING MECHANISM, INORGANIC CARBON, PCC6803, PHOTOSYNTHESIS, REGION, RUBULOSE-1,5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SP STRAIN PCC-7942, SUBUNIT, SYNECHOCOCCUS, TRANSPORT

2032

Ronentarazi, M., J. Liemanhurwitz, C. Gabay, M.I. Orus, and A. Kaplan. 1995. The genomic region of *rbclS* in *synechococcus* sp pcc-7942 contains genes involved in the ability to grow under low CO₂ concentration and in chlorophyll biosynthesis. *Plant Physiology* 108(4):1461-1469.

Several genes involved in the ability of *Synechococcus* sp. PCC 7942 to grow under different CO₂ concentrations were mapped in the genomic region of *rbclS* (the operon encoding the large and small subunits of ribulose-1,5-bisphosphate carboxylase/oxygenase). Insertion of a cartridge encoding kanamycin resistance within open reading frame (ORF) 78, designated *ccmJ*, located 7 kb upstream of *rbclS*, resulted in a kanamycin-resistant, high-CO₂-requiring mutant, M3, which does not contain normal carboxysomes. *ccmJ* shows significant homology to *csoS1* encoding a carboxysomal shell polypeptide in *Thiobacillus neopolitanus*. Analysis of the polypeptide pattern of a carboxysome-enriched fraction indicated several differences between the wild type and the mutant. The amount of the ribulose-1,5-bisphosphate carboxylase/oxygenase subunits was considerably smaller in the carboxysomal fraction of the mutant when compared to the wild type. On the basis of the sequence analyses, ORF286 and ORF466, located downstream of *ccmJ* were identified as *chit* and *chlN*, respectively, which are involved in chlorophyll biosynthesis in the dark.

KEYWORDS: ANACYSTIS-NIDULANS, CARBOXYLASE-OXYGENASE, CARBOXYSOME, CYANOBACTERIA, INORGANIC-CARBON UPTAKE, MECHANISM, MICROALGAE, PCC7942, TRANSPORT

2033

Rosenqvist, E., H. Pedersen, and C.O. Ottosen. 1996. Effects of elevated CO₂ on growth and photosynthesis in *dendranthema grandiflorum*. *Plant Physiology* 111(2):355.

2034

Rosenthal, Y. 1998. Variations of ecosystem gas exchange in the rain forest mesocosm at Biosphere 2 in response to elevated CO₂. *Global Change Biology* 4(5):539-547.

The effects of elevated CO₂ on tropical ecosystems were studied in the artificial rain forest mesocosm at Biosphere 2, a large-scale and ecologically diverse experimental facility located in Oracle, Arizona. The ecosystem responses were assessed by comparing the whole-system net gas exchange (NEE) upon changing CO₂ levels from 900 to 450 ppmV. The day-NEE was significantly higher in the elevated CO₂ treatment. In both experiments, the NEE rates were similar to values observed in natural analogue systems. Variations in night-NEE, reflecting both soil CO₂ efflux and plants respiration, covaried with temperature but showed no clear correlation with atmospheric CO₂ levels. After correcting for

changes in CO₂ efflux we show that the rain forest net photosynthesis increased in response to increasing atmospheric CO₂. The photosynthetic enhancement was expressed in higher quantum yields, maximum assimilation rates and radiation use efficiency. The results suggest that photosynthesis in large tropical trees is CO₂ sensitive, at least following short exposures of days to weeks. Taken at face value, the data suggest that as a result of anthropogenic emissions of CO₂, tropical rain forests may shift out of steady state, and become a carbon sink at least for short periods. However, a better understanding of the unique conditions and phenomena in Biosphere 2 is necessary before these results are broadly useful.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, MODEL

2035

Rosenthal, Y., B. Farnsworth, F.V.R. Romo, G.H. Lin, and B.D.V. Marino. 1999. High quality, continuous measurements of CO₂ in Biosphere 2 to assess whole mesocosm carbon cycling. *Ecological Engineering* 13(1-4):249-262.

Accurate measurements of atmospheric CO₂ concentrations are performed routinely in a variety of experimental settings including open fields and forests, leaf gas-exchange chambers, phytotrons and specialized growth chambers. However, the accurate monitoring of large scale structurally and biologically complex experimental systems, operating as materially closed systems, is not widely reported. Here we report the design elements, material specifications and other details for high precision monitoring of CO₂ in Biosphere 2, a large scale ecologically diverse experimental facility located in Oracle, AZ. The results are used to illustrate how carbon balance in a temporarily isolated sub-system of the facility is used to assess carbon dynamics under different environmental conditions such as variable atmospheric CO₂ levels, temperature, light, and soil moisture. The analytical system described here should be applicable for any settings in which continuous, high accuracy measurements of CO₂ in a complex system are needed for quantitative research. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: ACCLIMATION, ELEVATED CO₂, FOREST, GAS-EXCHANGE

2036

Rosenzweig, C., and D. Hillel. 1993. Agriculture in a greenhouse world. *Research & Exploration* 9(2):208-221.

While agriculture in some temperate regions may benefit from global climate change, tropical and subtropical regions may suffer. Even where potential production will improve, the required adjustments may disrupt ecosystems and land-use patterns. Agricultural zones will shift toward high latitudes, while heat stress and increased droughts will reduce productivity in lower latitudes. On the positive side, higher CO₂ may enhance photosynthesis and water-use efficiency. Future hazards include sea-level rise, insect infestation, and greater evaporation losses. Some agricultural activities augment the greenhouse effect by releasing CO₂, CH₄, and N₂O. Understanding the potential impacts of climate change is a prerequisite to developing societal responses.

KEYWORDS: CLIMATE CHANGE

2037

Rosenzweig, C., J. Phillips, R. Goldberg, J. Carroll, and T. Hodges. 1996. Potential impacts of climate change on citrus and potato production in the US. *Agricultural Systems* 52(4):455-479.

Potential impacts of global climate change on fruit and vegetable yield

in the US were investigated through simulations of citrus and potato. Simulated treatments included combinations of three increased temperature regimes (+1.5, +2.5 and +5.0 degrees C), and estimates of the impact of three levels of atmospheric carbon dioxide (440, 530, and 600 ppm) in addition to control runs representing current climatic conditions. Adaptive planting dates of -28, -14, +14 and +28 days were included in the potato simulations for current and increased temperature regimes. Twenty-two sites were simulated for citrus yields and 12 sites for potato, using climate records from 1951 to 1980. Response surfaces were developed for all combinations of increased temperature and CO₂. Results of citrus simulations without CO₂-induced yield improvement indicate that production may shift slightly northward in the southern states, but yields may decline in southern Florida and Texas due to excessive heat during the winter. CO₂ effects tended to counteract the decline in simulated citrus yields. Fall potato production under current management practices appears vulnerable to an increase in temperature in the northern states; increased CO₂ and changes in planting date were estimated to have minimal compensating impacts on simulated potato yields.

KEYWORDS: DARK RESPIRATION, DRY-MATTER PRODUCTION, ELEVATION, GROWTH, HEAT TOLERANCE, HIGH-TEMPERATURE, SOLANUM TUBEROSUM L, SOUR ORANGE TREES, WATER DEFICIT, YIELD PERFORMANCE

2038

Rosenzweig, C., and F.N. Tubiello. 1996. Effects of changes in minimum and maximum temperature on wheat yields in the central US - A simulation study. *Agricultural and Forest Meteorology* 80(2-4):215-230.

Recent observations and general circulation models indicate that future temperature changes linked to global warming might be characterized by a marked asymmetry between daytime maxima and nighttime minima. We investigate the importance of such a pattern in determining future wheat (*Triticum aestivum*) yields in the Central United States by using a dynamic crop growth model, CERES-Wheat, modified to include physiological effects of temperature and CO₂ on canopy photosynthesis. Simulations are run at four sites spanning a north-south transect of the Central US; four mean temperatures increases (1-4 degrees C) are applied to baseline daily climate data (1951-1980). The effects of two different scenarios of temperature change (minimum and maximum temperatures equally raised; minima increased three times as much as maxima in agreement with recent observations) are analyzed under both current (330 ppm) and elevated (550 ppm) CO₂ concentrations. The main mechanisms controlling the simulated wheat responses are direct and indirect temperature effects on wheat phenological development. Negative effects of temperature on simulated wheat yields are reduced when minima increase more than maxima. Yield changes are consistently negative under temperature change and current CO₂ concentration, while they range from positive to negative under temperature change and elevated CO₂ concentration. Responses vary across the transect, with larger negative effects occurring at the southernmost site.

KEYWORDS: CERES, CLIMATE CHANGE, CROP RESPONSE, MODEL

2039

Ross, D.J., S. Saggar, K.R. Tate, C.W. Feltham, and P.C.D. Newton. 1996. Elevated CO₂ effects on carbon and nitrogen cycling in grass/clover turves of a Psammaque soil. *Plant and Soil* 182(2):185-198.

Effects of elevated CO₂ (525 and 700 mu L L(-1)), and a control (350 mu L L(-1) CO₂), on biochemical properties of a Mollic Psammaque

soil in a well-established pasture of C3 and C4 grasses and clover were investigated with continuously moist turves in growth chambers over four consecutive seasonal temperature regimes from spring to winter inclusive. After a further 'spring' period, half of the turves under 350 and 700 mu L L(-1) were subjected to 'summer' drying and were then re-wetted before a further 'autumn' period; the remaining turves were kept continuously moist throughout these additional three consecutive 'seasons'. The continuously moist turves were then pulse-labelled with C-14-CO₂ to follow C pathways in the plant/soil system during 35 days. Growth rates of herbage during the first four 'seasons' averaged 4.6 g m(-2) day(-1) under 700 mu L L(-1) CO₂ and were about 10% higher than under the other two treatments. Below-ground net productivity at the end of these 'seasons' averaged 465, 800 and 824 g m(-2) in the control, 525 and 700 mu L L(-1) treatments, respectively. In continuously moist soil, elevated CO₂ had no overall effects on total, extractable or microbial C and N, or invertase activity, but resulted in increased CO₂-C production from soil, and from added herbage during the initial stages of decomposition over 21 days; rates of root decomposition were unaffected. CO₂ produced h(-1) mg(-1) microbial C was about 10% higher in the 700 mu L L(-1) CO₂ treatment than in the other two treatments. Elevated CO₂ had no clearly defined effects on N availability, or on the net N mineralization of added herbage. In the labelling experiment, relatively more C-14 in the plant/soil system occurred below ground under elevated CO₂, with enhanced turnover of C-14 also being suggested. Drying increased levels of extractable C and organic-N, but decreased mineral-N concentrations; it had no effect on microbial C, but resulted in lowered microbial N in the control only. In soil that had been previously 'summer'-dried, CO₂ production was again higher, but net N mineralization was lower, under elevated CO₂ than in the control after 'autumn' pasture growth. Over the trial period of 422 days, elevated CO₂ generally appears to have had a greater effect on soil C turnover than on soil C pools in this pasture ecosystem.

KEYWORDS: BIOCIDAL TREATMENTS, EXTRACTION METHOD, GRASS, LOLIUM-PERENNE, MICROBIAL BIOMASS, PASTURE TURVES, PLANTS, RHIZOSPHERE PH, SIMULATED SEASONAL-CHANGES, TEMPERATURE

2040

Ross, D.J., K.R. Tate, and P.C.D. Newton. 1995. Elevated co₂ and temperature effects on soil carbon and nitrogen cycling in ryegrass/white clover turves of an endoaquept soil. *Plant and Soil* 176(1):37-49.

Effects of elevated CO₂ (700 mu L L(-1)) and a control (350 mu L L(-1) CO₂) on the productivity of a 3-year-old ryegrass/white clover pasture, and on soil biochemical properties, were investigated with turves of a Typic Endoaquept soil in growth chambers. Temperature treatments corresponding to average winter, spring, and summer conditions in the field were applied consecutively to all of the turves. An additional treatment, at 700 mu L L(-1) CO₂ and a temperature 6 degrees C higher throughout than in the other treatments, was included. Under the same temperature conditions, overall herbage yields in the '700 mu L L(-1) CO₂' treatment were ca. 7% greater than in the control at the end of the 'summer' period. Root mass (to ca 25 cm depth) in the '700 mu L L(-1) CO₂' treatment was then about 50% greater than in the control, but in the '700 mu L L(-1) CO₂ + 6 degrees C' treatment it was 6% lower than in the control. Based on decomposition results, herbage from the '700 mu L L(-1) + 6 degrees C' treatment probably contained the highest proportion of readily decomposable components. Elevated CO₂ had no consistent effect on soil total C and N, microbial C and N, or extractable C concentrations in any of the treatments. Under the same temperature conditions, it did, however, enhance soil respiration (CO₂-C production) and invertase activity. The effects of elevated CO₂ on rates of net N mineralization were less distinct, and the apparent availability of N for the sward was not affected. Under elevated CO₂, soil in the higher-temperature treatment had a higher microbial C:N ratio; it also had a greater potential to degrade plant materials. Data interpretation was

complicated by soil spatial variability and the moderately high background levels of organic matter and biochemical properties that are typical of New Zealand pasture soils. More rapid cycling of C under CO₂ enrichment is, nevertheless, indicated. Further long-term experiments are required to determine the overall effect of elevated CO₂ on the soil C balance.

KEYWORDS: ATMOSPHERIC CO₂, BIOCIDAL TREATMENTS, CHLOROFORM, DECOMPOSITION, DIOXIDE, DIRECT EXTRACTION METHOD, FUMIGATION, MICROBIAL BIOMASS-C, MINERALIZATION, RESIDUES

2041

RossKarstens, G.S., G. Ebert, and P. Ludders. 1996. Diurnal time courses of CO₂ gas exchange in closed and open gas systems for coffee (*Coffea arabica* L.), pomegranate (*Punica granatum* L.), citrus (*Citrus limonia* Osb.), grape (*Vitis vinifera* L.), and banana (*Musa x paradisiaca* L.) in vitro plantlets under different environment conditions. *Journal of Applied Botany-Angewandte Botanik* 70(3-4):155-162.

Continuous measurements were made of CO₂ gas exchange over a period of three days on ill vitro plantlets of coffee (*Coffea arabica* L.), pomegranate (*Punica granatum* L.), citrus (*Citrus limonia* Osb.), grape (*Vitis vinifera* L.), and banana (*Musa x paradisiaca* L.). The gas used for measurements contained CO₂ concentrations of 350, 600, 1000 or 2000 $\mu\text{l l}^{-1}$. Measurements in the closed system for coffee plantlets grown in medium containing different sucrose concentrations showed a strong decrease of the CO₂ concentration in the cuvette atmosphere during the light period almost reaching the CO₂ compensation point (70 $\mu\text{l l}^{-1}$ CO₂). During the dark period a continuous increase was observed. Measured in the open system diurnal time courses of in vitro pomegranate and citrus plantlets showed that CO₂ assimilation rates were strongly influenced by light intensity and temperature. A positive balance of CO₂ gas exchange was found for pomegranate plantlets only with light intensities beyond 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetic photon flux density (PPFD). Citrus plantlets were independent of the sucrose concentration in the medium and showed a positive CO₂ balance at 350 $\mu\text{l l}^{-1}$ CO₂ gas concentration. Banana plantlets revealed negative balances under all conditions examined.

KEYWORDS: CULTURE, ENRICHMENT, GROWTH, INVITRO, PHOTOSYNTHETIC CHARACTERISTICS, TOBACCO

2042

RossKarstens, G.S., G. Ebert, and P. Ludders. 1996. Influence of CO₂ concentration, light intensity, and sucrose concentration on net photosynthesis of citrus plantlets during in vitro propagation. *Journal of Applied Botany-Angewandte Botanik* 70(5-6):188-193.

Light curves of the CO₂ gas exchange of in vitro plantlets of citrus (*Citrus limonia* Osb. (Rutaceae)) were measured continuously in an open system using different CO₂ concentrations (350, 1000, and 2000 $\mu\text{l l}^{-1}$ CO₂). The plantlets were grown in media with sucrose concentrations from 0 to 5% under light intensities of 60, 100, and 260 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Before starting the measurements the plantlets were pretreated with 1000 $\mu\text{l l}^{-1}$ CO₂ for several weeks. Control plantlets were grown for the same period in gas tight vessels. CO₂ concentration of the gas atmosphere inside the plant vessels had a stronger influence on CO₂ gas exchange of citrus plantlets than sucrose concentration of the medium. Net photosynthesis of plantlets grown under various light intensities differed only little when using the same CO₂ concentration for measurement as used for growing. After pretreatment with 1000 $\mu\text{l l}^{-1}$ CO₂ during growth, net photosynthesis of plantlets measured under 350 $\mu\text{l l}^{-1}$ CO₂ was higher compared to control plantlets.

KEYWORDS: ASPARAGUS, CARBON DIOXIDE, CULTURE,

ENRICHMENT, GROWTH, INVITRO

2043

Roth, S.K., and R.L. Lindroth. 1994. Effects of CO₂-mediated changes in paper birch and white-pine chemistry on gypsy-moth performance. *Oecologia* 98(2):133-138.

We examined the effects of CO₂-mediated changes in the foliar chemistry of paper birch (*Betula papyrifera*) and white pine (*Pinus strobus*) on performance of the gypsy moth (*Lymantria dispar*). Trees were grown under ambient or enriched CO₂ conditions, and foliage was subjected to plant chemical assays and insect bioassays. Enriched CO₂ atmospheres reduced foliar nitrogen levels and increased condensed tannin levels in birch but not in pine. Foliar carbohydrate concentrations were not markedly altered by CO₂ environment. Gypsy moth performance was significantly affected by CO₂ level, species, and the CO₂ x species interaction. Under elevated CO₂ conditions, growth was reduced for larvae fed birch, while development was prolonged for larvae fed pine. Although gypsy moths performed better overall on birch than pine, birch-fed larvae were influenced more by CO₂-mediated changes in host quality.

KEYWORDS: CARBON NUTRIENT BALANCE, CHEMICAL DEFENSE, CO₂, NITROGEN, PLANTS, PROTEIN, RESOURCE AVAILABILITY, TURNOVER

2044

Roth, S.K., and R.L. Lindroth. 1995. Elevated atmospheric CO₂ effects on phytochemistry, insect performance and insect parasitoid interactions. *Global Change Biology* 1(3):173-182.

This study was conducted to examine the effects of CO₂-mediated changes in tree chemistry on the performance of the gypsy moth (*Lymantria dispar* L.) and the parasitoid *Cotesia melanoscela* (Ratz.). We used carbon-nutrient balance theory to develop hypotheses regarding changes in tree chemistry and the performance of both insects under elevated CO₂. As predicted, levels of foliar nitrogen declined and concentrations of carbon-based compounds (e.g. starch and phenolics) increased under elevated CO₂. Gypsy moth performance (e.g. growth, development) was altered by CO₂-mediated changes in foliar chemistry, but the magnitude was small and varied across tree species. Larvae feeding on high CO₂ aspen exhibited the largest reduction in performance, relative to larvae feeding on birch, oak, or maple. Parasitism by *C. melanoscela* significantly prolonged gypsy moth development and reduced growth rates. Overall, the effect of parasitism on gypsy moth performance did not differ between CO₂ treatments. Altered gypsy moth performance on high CO₂ foliage in turn affected parasitoid performance, but the response was variable: parasitoid mortality increased and adult female size declined slightly under high CO₂, while development time and adult male size were unaffected. Our results suggest that CO₂-induced changes in plant chemistry were buffered to the extent that effects on third trophic level interactions were weak to non-existent for the system examined in this study.

KEYWORDS: CARBON NUTRIENT BALANCE, DEFENSE, DIET, NITROGEN, PLANTS, PROTEIN, TREES

2045

Roth, S., R.L. Lindroth, J.C. Volin, and E.L. Kruger. 1998. Enriched atmospheric CO₂ and defoliation: effects on tree chemistry and insect performance. *Global Change Biology* 4(4):419-430.

We examined the effects of CO₂ and defoliation on tree chemistry and performance of the forest tent caterpillar, *Malacosoma disstria*. Quaking aspen (*Populus tremuloides*) and sugar maple (*Acer saccharum*) trees

were grown in open-top chambers under ambient or elevated concentrations of CO₂. During the second year of growth, half of the trees were exposed to free-feeding forest tent caterpillars, while the remaining trees served as nondefoliated controls. Foliage was collected weekly for phytochemical analysis. Insect performance was evaluated on foliage from each of the treatments. At the sampling date coincident with insect bioassays, levels of foliar nitrogen and starch were lower and higher, respectively, in high CO₂ foliage, and this trend persisted throughout the study. CO₂-mediated increases in secondary compounds were observed for condensed tannins in aspen and gallotannins in maple. Defoliation reduced levels of water and nitrogen in aspen but had no effect on primary metabolites in maple. Similarly, defoliation induced accumulations of secondary compounds in aspen but not in maple. Larvae fed foliage from the enriched CO₂ or defoliated treatments exhibited reduced growth and food processing efficiencies, relative to larvae on ambient CO₂ or nondefoliated diets, but the patterns were host species-specific. Overall, CO₂ and defoliation appeared to exert independent effects on foliar chemistry and forest tent caterpillar performance.

KEYWORDS: BIRCH, CARBON NUTRIENT BALANCE, COVARIANCE, FOLIAGE, HERBIVORE RESPONSES, INDUCTION, MOTH, NITROGEN, PHYTOCHEMISTRY, PLANTS

2046

Roth, S., E.P. McDonald, and R.L. Lindroth. 1997. Atmospheric CO₂ and soil water availability: consequences for tree-insect interactions. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 27(8):1281-1290.

The consequences of elevated CO₂ for interactions between trees and associated insects will be influenced by the availability of other plant resources. We investigated the effects of CO₂ and water availability on phytochemistry of quaking aspen (*Populus tremuloides* Michx.) and sugar maple (*Acer saccharum* Marsh.) and the associated performance of the forest tent caterpillar (*Malacosoma disstria* Hbn.). Seedlings were grown under ambient or elevated CO₂ concentrations and under well-watered or drought conditions. We measured rates of gas exchange and subjected foliage to phytochemical assays. Bioassays were conducted to quantify larval performance on foliage from the various treatments. In general, elevated CO₂ increased photosynthetic rates and had no effect on stomatal conductance, while drought reduced both parameters. Foliar nitrogen levels declined and secondary metabolite concentrations increased under enriched CO₂, but starch and sugar levels were unaffected. All phytochemicals measured, with the exception of simple sugars, declined or did not change in response to drought. CO₂- and drought-mediated changes in phytochemistry reduced forest tent caterpillar growth and food processing efficiencies, but the patterns were host-species specific. This work demonstrates that CO₂ effects on forest trees will be mediated by the availability of water and that the direction and magnitude of responses will depend on the tree species involved, which will, in turn, affect patterns of host use by herbivorous insects.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO₂, GAS-EXCHANGE, GROWTH, HERBIVORE INTERACTIONS, LEPIDOPTERA, PHOTOSYNTHESIS, RESPONSES, SEEDLINGS, STRESS

2047

Rothschild, L.J. 1994. Elevated CO₂ - impact on diurnal patterns of photosynthesis in natural microbial ecosystems. *Life Sciences and Space Research XXV (3)* 14(11):285-289.

Algae, including blue-green algae (cyanobacteria), are the major source of fixed carbon in many aquatic ecosystems. Previous work has shown that photosynthetic carbon fixation is often enhanced in the presence of

additional carbon dioxide (CO₂). This study was undertaken to determine if this CO₂ fertilization effect extended to microbial mats, and, if so, at what times during the day might the addition of CO₂ affect carbon fixation. Four microbial mats from diverse environments were selected, including mats from a hypersaline pond (area 5, Exportadora de Sal, Mexico), the marine intertidal (Lyngbya, Laguna Ojo de Liebre, Mexico), an acidic hot spring (Cyanidium, Nymph Creek, Yellowstone National Park), and an acidic stream at ambient temperature (Zygonium, Yellowstone National Park). Carbon fixation in the absence of additional CO₂ essentially followed the rising and falling sunlight levels, except that during the middle of the day there was a short dip in carbon fixation rates. The addition of CO₂ profoundly enhanced carbon fixation rates during the daylight hours, including during the midday dip. Therefore, it is unlikely that the midday dip was due to photoinhibition. Surprisingly, enhancement of carbon fixation was often greatest in the early morning or late afternoon, times when carbon fixation would be most likely to be light limited.

KEYWORDS: CARBON FIXATION, MARINE MACROALGAE, MAT, MODEL, OXYGENIC PHOTOSYNTHESIS

2048

Rotter, R., and S.C. Van de Geijn. 1999. Climate change effects on plant growth, crop yield and livestock. *Climatic Change* 43(4):651-681.

A review is given of the state of knowledge in the field of assessing climate change impacts on agricultural crops and livestock. Starting from the basic processes controlling plant growth and development, the possible impacts and interactions of climatic and other biophysical variables in different agro- environments are highlighted. Qualitative and quantitative estimations of shifts in biomass production and water relations, inter-plant competition and crop species adaptability are discussed. Special attention is given to the problems encountered when scaling up physiological responses at the leaf- and plant level to yield estimates at regional to global levels by using crop simulation models in combination with geo-referenced, agro-ecological databases. Some non-linear crop responses to environmental changes and their relations to adaptability and vulnerability of agro-ecosystems are discussed.

KEYWORDS: AIR- TEMPERATURE, ATMOSPHERIC CO₂ ENRICHMENT, B RADIATION, ELEVATED CARBON-DIOXIDE, GLOBAL ENVIRONMENT CHANGE, LEAF-AREA, RESPONSES, TEMPERATURE-GRADIENT CHAMBERS, WATER-USE, WINTER-WHEAT

2049

Rotzel, C., P.W. Leadley, and C. Korner. 1997. Non-destructive assessment of the effects of elevated CO₂ on plant community structure in a calcareous grassland. *Acta Oecologica-International Journal of Ecology* 18(3):231-239.

Calcareous grassland was exposed to ambient or elevated CO₂ using a Screen-Aided CO₂ Control (SACC) system starting in March 1994. The effects of elevated CO₂ on plant community structure were studied using the point intercept method. Measurements were made in March 1994 prior to the start of CO₂ exposure and again in June 1994 at peak plant biomass. There were no significant differences in the initial structure of the communities based on their assigned CO₂ treatments in March. After 9 weeks of exposure of the community to elevated CO₂, the total number of intercepts per plot was not significantly different between CO₂ treatments; however, *Carex flacca* and *Cirsium acaule* had marginally significant ($P = 0.055$ and $P = 0.06$) increases in the % sward of the community at elevated CO₂ (number of intercepts for a single species divided by the total number of intercepts for all species). Measurements of leaf extension in *Carex flacca* showed that at least part of the increase in % sward at elevated CO₂ could be explained by

greater leaf length per plant ($P = 0.02$). These measurements and other experiments with calcareous grassland species and communities suggest that rising atmospheric CO₂ concentrations will probably alter the structure of calcareous grassland communities.

KEYWORDS: ATMOSPHERIC CO₂, ENRICHMENT, GROWTH

2050

Rouhier, H., G. Billes, L. Billes, and P. Bottner. 1996. Carbon fluxes in the rhizosphere of sweet chestnut seedlings (*Castanea sativa*) grown under two atmospheric CO₂ concentrations: C-14 partitioning after pulse labelling. *Plant and Soil* 180(1):101-111.

Partitioning of C-14 was assessed in sweet chestnut seedlings (*Castanea sativa* Mill.) grown in ambient and elevated atmospheric [CO₂] environments during two vegetative cycles. The seedlings were exposed to (CO₂)-C-14 atmosphere in both high and low [CO₂] environments for a 6-day pulse period under controlled laboratory conditions. Six days after exposure to (CO₂)-C-14, the plants were harvested, their dry mass and the radioactivity were evaluated. C-14 concentration in plant tissues, root-soil system respiratory outputs and soil residues (rhizodeposition) were measured. Root production and rhizodeposition were increased in plants growing in elevated atmospheric [CO₂]. When measuring total respiration, i.e. CO₂ released from the root/soil system, it is difficult to separate CO₂ originating from roots and that coming from the rhizospheric microflora. For this reason a model accounting for kinetics of exudate mineralization was used to estimate respiration of rhizospheric microflora and roots separately. Root activity (respiration and exudation) was increased at the higher atmospheric CO₂ concentration. The proportion attributed to root respiration accounted for 70 to 90% of the total respiration. Microbial respiration was related to the amount of organic carbon available in the rhizosphere and showed a seasonal variation dependent upon the balance of root exudation and respiration. The increased carbon assimilated by plants grown under elevated atmospheric [CO₂] stayed equally distributed between these increased root activities.

KEYWORDS: DIOXIDE, ELEVATED CO₂, ENRICHMENT, MICROBIAL BIOMASS, NITROGEN, RESPIRATION, ROOT, SOIL, SPRING WHEAT, TURNOVER

2051

Rouhier, H., G. Billes, A. Elkohen, M. Mousseau, and P. Bottner. 1994. Effect of elevated CO₂ on carbon and nitrogen distribution within a tree (*castanea-sativa* mill) soil system. *Plant and Soil* 162(2):281-292.

Two-year-old sweet chestnut trees were grown outside in normal or double CO₂ atmospheric concentration. In spring and in autumn of two growing seasons, a six day labelling pulse of C-14 labelled CO₂ was used to follow the carbon assimilation and distribution in the plant-soil system. Doubling atmospheric CO₂ had a significant effect on the tree net carbon uptake. A large proportion of the additional C uptake was 'lost' through the root system. This suggests that increased C uptake under elevated CO₂ conditions increases C cycling without necessarily increasing C storage in the plant. Total root derived material represented a significant amount of the 'extra-assimilated' carbon due to the CO₂ treatment and was strongly correlated with the phenological stage of the tree. Increasing root rhizodeposition led to a stimulation of microbial activity, particularly near the end of the growing season. When plant rhizodeposition was expressed as a function of the root dry weight, the effect of increasing CO₂ resulted in a higher root activity. The C to N ratios were significantly higher for trees grown under elevated CO₂ except for the fine root compartment. An evaluation of the plant-soil system nitrogen dynamics showed, during the second season of CO₂ treatment, a decrease of soil N mineralization rate and total N uptake for trees grown at elevated CO₂ levels.

KEYWORDS: ATMOSPHERIC CO₂, DIOXIDE, ENRICHMENT, GROWTH, PLANTS, QUERCUS-ALBA, RESPIRATION, RHIZOSPHERE, SEEDLINGS, TURNOVER

2052

Rouhier, H., and D.J. Read. 1998. Plant and fungal responses to elevated atmospheric carbon dioxide in mycorrhizal seedlings of *Pinus sylvestris*. *Environmental and Experimental Botany* 40(3):237-246.

The effects of elevated CO₂ concentration upon the mycorrhizal relationships of Scots pine (*Pinus sylvestris*) seedlings were investigated. Plants were grown for 4 months with their shoots exposed to ambient (C-AMB = 360 μ mol l⁻¹) or elevated (C-ELEV = 700 μ mol l⁻¹) CO₂ environments while their root systems, either colonised by the mycorrhizal fungi *Paxillus involutus* or *Suillus bovinus*, or left in the non-mycorrhizal condition, were maintained in sealed dishes. In one series of these plants the effects of C-ELEV upon the extent of mycorrhizal development and upon their growth and nutrition were determined, while another series were transferred from the dishes after 1 month, to transparent observation chambers before being returned to the two CO₂ environments. In these chambers, the effects of C-ELEV upon development of the external mycelial systems of the two mycorrhizal fungi was determined by measuring the advance of the hyphal fronts of the mycorrhizal fungi across non-sterile peat from the colonised plants. The dry mass and number of mycorrhizal tips were significantly higher in C-ELEV than in the C-AMB condition in plants colonised by both fungi in the dishes. Yields of whole plants and of shoots were higher in the C-ELEV treatment whether or not they were grown in the mycorrhizal condition, but the greater yields were not associated in these sealed systems with enhanced nutrient gain. The dry mass of non-mycorrhizal plants was greater than that of those colonised by mycorrhizal fungi under elevated CO₂. This is thought to be attributable to the energetic cost of production of the larger mycorrhizal systems in this treatment. The extent of development of the mycorrhizal mycelial systems of both fungi was greatly increased in C-ELEV relative to that in C-AMB environments. It is hypothesised that increased allocation of carbon to mycorrhizal root systems and their associated mycelia would provide the potential for enhancement of nutrient acquisition in open systems of greater fertility. (C) 1998 Elsevier Science B.V. All rights reserved.

KEYWORDS: CO₂, DYNAMICS, ECTOMYCORRHIZAL COLONIZATION, GROWTH, JUVENILE PONDEROSA PINE, MYCELIUM, NITROGEN, ROOTS, SOIL N

2053

Rouhier, H., and D.J. Read. 1998. The role of mycorrhiza in determining the response of *Plantago lanceolata* to CO₂ enrichment. *New Phytologist* 139(2):367-373.

Plantago lanceolata L. was grown for 104 d with (M) or without (NM) arbuscular mycorrhizal colonization under conditions of ambient (C-AMB = 350 μ mol l⁻¹) and elevated (C-ELEV = 540 μ mol l⁻¹) CO₂. Sequential harvests (H) were taken at 41 (H-1), 76 (H-2) and 104 d (H-3) to determine the time-course of mycorrhizal influence on the response of the plant to CO₂ enrichment. Total yields of M plants were greater than those of NM from H-2 onwards. Plants in the M-ELEV treatment were significantly larger than those in the M-AMB at 104 d. There were significant but much smaller differences in yield between NMELEV and NMAMB. The differences in total yield arose through impact of C-ELEV on both shoots and roots. Total root length was greater in M-ELEV than in M-AMB only at H-3, but total length of mycorrhizal root was greater at H-2 and H-3. The percentages of root length colonized and that occupied by arbuscules and vesicles were greater in M-ELEV than in M-AMB at the last two harvests, indicating increased sequestration of carbon in internal fungal structures. Though extraradical

hyphal lengths were greater in M-ELEV than in M-AMB at H-2 and H-3, the differences were not significant. Phosphorus inflow and P content of M plants were higher than those of NM plants at H-2 and H-3, and were higher in M-ELEV than in M-AMB at H-3. ANOVA revealed no significant interactions between CO₂ and mycorrhizal treatment. The results are discussed in relation to carbon sequestration in mycorrhizal systems and likely impacts of CO₂ enrichment on *P. lanceolata* grown under field conditions. The importance of sequential harvesting for realistic determination of responses to CO₂ is stressed.

KEYWORDS: *BOUTELOUA-GRACILIS, CARBON DIOXIDE, COLONIZATION, COMMUNITY, DIVERSITY, ECOSYSTEMS, ELEVATED ATMOSPHERIC CO₂, FUNGI, RHIZOSPHERE, ROOTS*

2054

Rouhier, H., and D.J. Read. 1999. Plant and fungal responses to elevated atmospheric CO₂ in mycorrhizal seedlings of *Betula pendula*. *Environmental and Experimental Botany* 42(3):231-241.

The effects of elevated CO₂ concentrations upon carbon allocation in mycorrhizal (M) and non-mycorrhizal (NM) birch (*Betula pendula*) seedlings were investigated. M plants, colonised by the fungus *Paxillus involutus*, and NM plants, were exposed for 3 months to ambient (350 $\mu\text{mol l}^{-1}$) or elevated (700 $\mu\text{mol l}^{-1}$) CO₂ environments. The assimilation and distribution of carbon within the different compartments of the plant-substrate-fungal system were investigated using radioactive carbon as a tracer. In addition, the impact of elevated CO₂ upon extension growth of the ectomycorrhizal mycelium of the fungus was determined in transparent observation chambers. Yields of whole plants and of shoots were significantly decreased under elevated CO₂ whether they were grown with or without their fungal symbionts. Neither the dry mass production of roots of mycorrhizal plants, nor the amount of carbon allocated to shoots, roots and mycorrhizal tips were affected by elevated CO₂. While the number of mycorrhizal root tips was decreased with CO₂ enrichment, their relative importance in the total root system was unchanged. There was a significant increase in the extent of development of the external mycelium under elevated CO₂. A greater proportion of the radioactive carbon was allocated to the soil compartment under elevated CO₂. This increase, probably arising through increased rhizodeposition, was greater in NM than M plants. The responses are discussed in terms of nutrient availability in the growth media and the possible role of increased carbon allocation to mycorrhizal mycelium in nature. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: *ALLOCATION, AVAILABILITY, CARBON-DIOXIDE CONCENTRATION, COLONIZATION, ENRICHMENT, GROWTH, NITROGEN, PHOTOSYNTHESIS, PINE SEEDLINGS, ROTH*

2055

Roumet, C., M.P. Bel, L. Sonie, F. Jardon, and J. Roy. 1996. Growth response of grasses to elevated CO₂: A physiological plurispecific analysis. *New Phytologist* 133(4):595-603.

The effect of CO₂ enrichment on the growth and the economy of carbon and nitrogen of 11 Mediterranean grass species was investigated in order to determine the underlying causes of the large variation observed between species in their responses to elevated CO₂. Plants were grown for 26-43 d (depending on species growth rate) under productive conditions at ambient (350 $\mu\text{mol mol}^{-1}$) and elevated (700 $\mu\text{mol mol}^{-1}$) concentrations of CO₂. Plant parameters were determined at a common biomass of 0.15 g to determine the CO₂ effect independent of ontogenic effects. The effect of CO₂ on RGR ranged from -6.7 to 22.5%, with a mean stimulation of 10.3%. Averaged over the 11 species, the growth enhancement resulted from an increase in net assimilation rate per unit leaf d. wt. (NAR(w)) of 10.6%. This was the result of a

large increase (18.7%) in NAR per unit leaf area (NAR(a)) associated with a 8.1% decrease in the specific leaf area (SLA). This decrease in SLA was due to a large increase of the non-structural carbohydrates. The increase in shoot activity was balanced by a 7.6% increase in the specific absorption rate of nitrogen (SAR). As a result, plant nitrogen content was not modified. Leaf nitrogen productivity was significantly increased (14.9%). Shoot vs. root allocation of biomass and nitrogen was not modified. An analysis across the 11 species of the relationships between the stimulation of RGR and the alteration in RGR components showed a significant correlation only with increases in NAR(w), SAR and nitrogen productivity. The co-ordinated increase in these three parameters constitutes a single response syndrome, whose intensity is responsible for most of the species variability.

KEYWORDS: *ATMOSPHERIC CO₂, BIOMASS ALLOCATION, C-3, CARBON DIOXIDE, ENRICHMENT, NITROGEN CONCENTRATION, NUTRITION, PHOTOSYNTHESIS, PLANT GROWTH, ROOT*

2056

Roumet, C., G. Laurent, and J. Roy. 1999. Leaf structure and chemical composition as affected by elevated CO₂: genotypic responses of two perennial grasses. *New Phytologist* 143(1):73-81.

Genotypic variability was studied in two Mediterranean grass species, *Bromus erectus* and *Dactylis glomerata*, with regard to the response to CO₂ of leaf total non-structural carbohydrate concentration ([TNC](1f)), specific leaf area (SLA), and leaf carbon and nitrogen concentrations ([C](1f) and [N](1f), respectively). Fourteen genotypes of each species were grown together on intact soil monoliths at ambient and elevated CO₂ concentrations (350 and 700 $\mu\text{mol mol}^{-1}$, respectively). In both species, the most consistent effect of elevated CO₂ was an increase in [TNC](1f) and a decrease in leaf nitrogen concentration when expressed either as total dry mass [N- m](1f), structural dry mass [N(m)st](1f) or leaf area [N- a](1f). The SLA decreased only in *D. glomerata*, due to an accumulation of total nonstructural carbohydrates and to an increase in leaf density. No genotypic variability was found for any variable in *B. erectus*, suggesting that genotypes responded in a similar way to elevated CO₂. In *D. glomerata*, a genotypic variability was found only for [Cst], [N-m](1f), [N(m)st](1f) and [N-a](1f). Since [N-m](1f) is related to plant growth and is a strong determinant of plant-herbivore interactions, our results suggest evolutionary consequences of elevated CO₂ through competitive interactions or herbivory.

KEYWORDS: *ARABIDOPSIS-THALIANA, ATMOSPHERIC CO₂, CARBON DIOXIDE, ENRICHMENT, GROWTH-RESPONSE, INTRASPECIFIC VARIATION, LITTER QUALITY, NITROGEN CONCENTRATION, NUTRIENT, PLANTAGO-MAJOR*

2057

Roumet, C., and J. Roy. 1996. Prediction of the growth response to elevated CO₂: A search for physiological criteria in closely related grass species. *New Phytologist* 134(4):615-621.

Using 11 closely related grass species, we tested the capacity of physiological criteria to predict the growth response to elevated CO₂ and to categorize the species with regard to their CO₂ response. A growth analysis was conducted under productive conditions both at ambient (350 $\mu\text{mol mol}^{-1}$) and elevated (700 $\mu\text{mol mol}^{-1}$) CO₂. The relative growth rate stimulation was regressed against each of the growth rate components measured at ambient CO₂. Growth response to CO₂ was positively correlated with specific leaf area (SLA, the leaf surface area per unit of leaf weight), leaf area ratio (the leaf area per unit of total plant dry weight) and negatively correlated with net assimilation rate and leaf nitrogen concentration, both per unit of leaf area. We suggest that SLA has a predominant role in these relationships. Different hypotheses are proposed and discussed in order to explain why species with low

SLA are less responsive to elevated CO₂. Neither biomass allocation, relative growth rate, shoot or root specific activities per unit of mass, nor chemical composition were significantly correlated with growth response to CO₂. The four predictive criteria mentioned above coherently differentiate the five wild annual species (higher SLA, stronger growth response to CO₂) from the four wild perennials. The two perennial crop species, with the highest SLA, were more responsive than the wild species.

KEYWORDS: AMBIENT, ARABIDOPSIS-THALIANA, ASSIMILATION RATE, BIOMASS, CARBON-DIOXIDE ENRICHMENT, LEAVES, NITROGEN, PHOTOSYNTHESIS, PLANTS, TEMPERATURE

2058

Rousopoulos, D., A. Liakatas, and W.J. Whittington. 1998. Cotton responses to different light-temperature regimes. *Journal of Agricultural Science* 131:277-283.

A series of experiments investigating the interactive effects of light and temperature on vegetative growth, earliness, fruiting, yield and fibre properties in three cultivars of cotton, was undertaken in growth rooms. Two constant day/night temperature regimes with a difference of 4 degrees C (30/20 and 26/16.5 degrees C) were used throughout the growing season in combination with two light intensities (75 and 52.5 W m⁻²). The results showed that significant interactions occurred for most of the characters studied. Although the development of leaf area was mainly temperature-dependent, plants at harvest had a larger leaf area when high temperature was combined with low rather than with high light intensity. Leaf area was least in the low temperature-low light regime. However, the plants grown under the high temperature-low light combination weighed the least. Variations in the number of nodes and internode length were largely dependent on temperature rather than light. Light did, however, affect the numbers of branches, sympodia and monopodia. The first two of these were highest in the high light-high temperature regime and the third in the low light- low temperature regime. All other characters, except time to certain developmental stages and fibre length, were reduced at the lower light intensity. Variation in temperature modified the light effect and vice versa, in a character-dependent manner. More specifically, square and boll dry weights, as well as seed cotton yield per plant, were highest in high light combined with low temperature, where the most and heaviest bolls were produced. But flower production was favoured by high light and high temperature, suggesting increased boll retention at low temperature, especially when combined with low light. Low temperature and high light also maximized lint percentage. Fibres were shortest in the high temperature-high light regime, where fibre strength, micronaire index and maturity ratio were at a maximum. However, the finest and the most uniform fibres were produced when high light was combined with low temperature. Cultivar differences were significant mainly in leaf area and dry matter production at flowering.

KEYWORDS: AIR CO-2 ENRICHMENT, CANOPY PHOTOSYNTHESIS, FIELD, GROWTH, LEAF CONDUCTANCE, LEAVES, RESPIRATION, TRANSPIRATION, WATER-STRESS

2059

Rowlandbamford, A.J., L.H. Allen, J.T. Baker, and K.J. Boote. 1990. Carbon-dioxide effects on carbohydrate status and partitioning in rice. *Journal of Experimental Botany* 41(233):1601-1608.

The atmospheric carbon dioxide (CO₂) concentration has been rising and is predicted to reach double the present concentration sometime during the next century. The objective of this investigation was to determine the long-term effects of different CO₂ concentrations on carbohydrate status and partitioning in rice (*Oryza sativa* L. cv. IR-30). Rice plants were grown season-long in outdoor, naturally sunlit,

environmentally controlled growth chambers with CO₂ concentrations of 160, 250, 330, 500, 660, and 900 μ -mol CO₂ mol⁻¹ air. In leaf blades, the priority between the partitioning of carbon into storage carbohydrates or into export changed with development stage and CO₂ concentration. During vegetative growth, leaf sucrose and starch concentrations increased with increasing CO₂ concentration but tended to level off above 500 μ -mol mol⁻¹ CO₂. Similarly, photosynthesis also increased with CO₂ concentrations up to 500 μ -mol mol⁻¹ and then reached a plateau at higher concentrations. The ratio of starch to sucrose concentration was positively correlated with the CO₂ concentration. At maturity, increasing CO₂ concentration resulted in an increase in total non-structural carbohydrate (TNC) concentration in leaf blades, leaf sheaths and culms. Carbohydrates that were stored in vegetative plant parts before heading made a smaller contribution to grain dry weight at CO₂ concentrations below 330 μ -mol mol⁻¹ than for treatments at concentrations above ambient. Increasing CO₂ concentration had no effect on the carbohydrate concentration in the grain at maturity.

KEYWORDS: CO₂, ENRICHMENT, GROWTH, NITROGEN, PHOTOSYNTHESIS, PLANTS, STARCH, YIELD

2060

Rowlandbamford, A.J., J.T. Baker, L.H. Allen, and G. Bowes. 1991. Acclimation of rice to changing atmospheric carbon-dioxide concentration. *Plant, Cell and Environment* 14(6):577-583.

The effects were studied of season-long (75 and 88 d) exposure of rice (*Oryza sativa* L. cv. IR-30) to a range of atmospheric CO₂ concentrations in outdoor, computer-controlled, environment chambers under natural solar radiation. The CO₂ concentrations were maintained at 160, 250, 330, 500, 660 and 900- μ -mol mol⁻¹ air. Photosynthesis increased with increasing growth CO₂ concentrations up to 500- μ -mol mol⁻¹, but levelled off at higher CO₂ values. Specific leaf area also increased significantly with increasing CO₂. Although leaf dry weight and leaf area index increased, the overall response was not statistically significant. Leaf nitrogen content dropped slightly with elevated CO₂, but the response was not statistically significant. The specific activity of ribulose biphosphate carboxylase/oxygenase (rubisco) declined significantly over the CO₂ concentration range 160 to 900- μ -mol mol⁻¹. When expressed on a leaf area basis, rubisco activity decreased by 66%. This was accompanied by a 32% decrease in the amount of rubisco protein as a fraction of the total soluble leaf protein, and by 60% on a leaf area basis. For leaves in the dark, the total rubisco activity (CO₂/Mg²⁺-activated) was reduced by more than 60%. This indicates that rice accumulated an inhibitor in the dark, probably 2-carboxyarabinitol 1-phosphate (CA-1-P). However, the inhibitor did not seem to be involved in the acclimation response. The degree of carbamylation of the rubisco enzyme was unchanged by the CO₂ growth regime, except at 900- μ -mol mol⁻¹ where it was reduced by 24%. The acclimation of rice to different atmospheric CO₂ conditions involved the modulation of both the activity and amount of rubisco protein in the leaf.

KEYWORDS: ACTIVATION, ENRICHMENT, GROWTH, HIGH CO₂, INHIBITOR, LIGHT, MONOECIOUS CUCUMBERS, PHOTOSYNTHESIS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SOYBEAN LEAVES

2061

RowlandBamford, A.J., J.T. Baker, L.H. Allen, and G. Bowes. 1996. Interactions of CO₂ enrichment and temperature on carbohydrate accumulation and partitioning in rice. *Environmental and Experimental Botany* 36(1):111-124.

The objective of this study was to determine the long-term effects of CO₂ concentration and temperature on carbohydrate partitioning and

status in rice (*Oryza sativa* L. cv. IR-30). The plants were grown season-long in sunlit, controlled- environment chambers with CO₂ concentrations of 330 or 660 $\mu\text{mol mol}^{-1}$, and daytime air temperatures of 28, 34 or 40 degrees C. In leaf blades, the priority between partitioning of carbon into storage or into export changed with CO₂ concentration and temperature. Leaf sucrose concentration increased with CO₂ enrichment at all temperature regimes. Over the season, elevated CO₂ resulted in an increase in total non- structural carbohydrate (TNC) concentration in leaf blades, leaf sheaths and culms at all temperature treatments. Elevated CO₂ had no effect on carbohydrate concentration in the grain at maturity, however, grain TNC concentration was significantly lowered by increasing temperature. Under the highest temperature regime, the plants in the 330 $\mu\text{mol mol}^{-1}$ CO₂ treatment died during stem extension while the CO₂ enriched plants survived but produced sterile panicles. The results suggest that CO₂-enriched plants could survive and maintain carbohydrate production rates at higher temperatures than the non-enriched plants; however, the optimum temperature for TNC accumulation was 28 degrees C at both CO₂ concentrations.

KEYWORDS: AIR- TEMPERATURE, CARBON-DIOXIDE CONCENTRATION, CLIMATE SENSITIVITY, GROWTH, LEAVES, MODEL, OCEAN, RESPONSES

2062

Rozema, J. 1993. Plant-responses to atmospheric carbon-dioxide enrichment - interactions with some soil and atmospheric conditions. *Vegetatio* 104:173-190.

In general, C3 plant species are more responsive to atmospheric carbon dioxide (CO₂) enrichment than C4-plants. Increased relative growth rate at elevated CO₂ primarily relates to increased Net Assimilation Rate (NAR), and enhancement of net photosynthesis and reduced photorespiration. Transpiration and stomatal conductance decrease with elevated CO₂, water use efficiency and shoot water potential increase, particularly in plants grown at high soil salinity. Leaf area per plant and leaf area per leaf may increase in an early growth stage with increased CO₂, after a period of time Leaf Area Ratio (LAR) and Specific Leaf Area (SLA) generally decrease. Starch may accumulate with time in leaves grown at elevated CO₂. Plants grown under salt stress with increased (dark) respiration as a sink for photosynthates, may not show such acclimation to increased atmospheric CO₂ levels. Plant growth may be stimulated by atmospheric carbon dioxide enrichment and reduced by enhanced UV-B radiation but the limited data available on the effect of combined elevated CO₂ and ultraviolet B (280-320 nm) (UV-B) radiation allow no general conclusion. CO₂-induced increase of growth rate can be markedly modified at elevated UV-B radiation. Plant responses to elevated atmospheric CO₂ and other environmental factors such as soil salinity and UV-B tend to be species-specific, because plant species differ in sensitivity to salinity and UV-B radiation, as well as to other environmental stress factors (drought, nutrient deficiency). Therefore, the effects of joint elevated atmospheric CO₂ and increased soil salinity or elevated CO₂ and enhanced UV-B to plants are physiologically complex.

KEYWORDS: AIR- TEMPERATURE, B RADIATION, CO₂-ENRICHMENT, DIFFERENT IRRADIANCES, ELEVATED CO₂, ESTUARINE MARSH, GROWTH, PHOTOSYNTHESIS, STRESS, WATER RELATIONS

2063

Rozema, J., F. Dorel, R. Janissen, G. Lenssen, R. Broekman, W. Arp, and B.G. Drake. 1991. Effect of elevated atmospheric CO₂ on growth, photosynthesis and water relations of salt-marsh grass species. *Aquatic Botany* 39(1-2):45-55.

The C3 grass species *Scirpus maritimus* L. and *Puccinellia maritima* (Huds.) Parl., and the C4 grass species *Spartina anglica* C.E. Hubbard and *Spartina patens* (Ait.) Muhl. were grown at ambient (340 p.p.m. CO₂) and elevated (580 p.p.m. CO₂) atmospheric CO₂ concentration, at low (10 mM NaCl) and high salinity (250 mM NaCl) under aerated and anaerobic conditions in the culture solution. The relative growth rate of both the C3 grass species was enhanced with atmospheric CO₂ enrichment, no such increase was found in the C4 grass species. High salinity reduced growth of the C3 species tested, but this relative growth reduction was not prevented by elevated CO₂ concentration. The growth increase at elevated CO₂ of *Scirpus maritimus* and *Puccinellia maritima* is greater under aerated than under anaerobic solution conditions. Water-use efficiency of all species was increased by elevated CO₂. In the case of *Scirpus* (C3), this increase was caused by increased net photosynthesis, for *Spartina patens* (C4) photosynthesis was not increased, but transpiration was reduced. The water potential of the shoot was less negative under conditions of CO₂ enrichment, in particular at increased salinity (250 mM NaCl).

KEYWORDS: C-4 PLANTS, CARBON DIOXIDE, ENRICHMENT, ESTUARINE MARSH, NITROGEN, PLANT GROWTH, TEMPERATURE

2064

Rozema, J., G.M. Lenssen, J.W.M. vandeStaij, M. Tosserams, A.J. Visser, and R.A. Broekman. 1997. Effects of UV-B radiation on terrestrial plants and ecosystems: Interaction with CO₂ enrichment. *Plant Ecology* 128(1-2):182-191.

UV-B radiation is just one of the environmental factors, that affect plant growth. It is now widely accepted that realistic assessment of plant responses to enhanced UV-B should be performed at sufficiently high Photosynthetically Active Radiation (PAR), preferably under field conditions. This will often imply, that responses of plants to enhanced UV-B in the field will be assessed under simultaneous water shortage, nutrient deficiency and variation of temperature. Since atmospheric CO₂ enrichment, global warming and increasing UV-B radiation represent components of global climatic change, interactions of UV-B with CO₂ enrichment and temperature are particularly relevant. Only few relevant UV-B x CO₂ interaction studies have been published. Most of these studies refer to greenhouse experiments. We report a significant CO₂ x UV-B interaction for the total plant dry weight and root dry weight of the C-3-grass *Elymus athericus*. At elevated CO₂ (720 $\mu\text{mol mol}^{-1}$), plant growth was much less reduced by enhanced UV-B than at ambient atmospheric CO₂ although there were significant (positive) CO₂ effects and (negative) UV-B effects on plant growth. Most other CO₂ x UV-B studies do not report significant interactions on total plant biomass. This lack of CO₂ x UV-B interactions may result from the fact that primary metabolic targets for CO₂ and UVB are different. UV-B and CO₂ may differentially affect plant morphogenetic parameters: biomass allocation, branching, flowering, leaf thickness, emergence and senescence. Such more subtle interactions between CO₂ and UV-B need careful and long term experimentation to be detected. In the case of no significant CO₂ x UV-B interactions, combined CO₂ and UV-B effects will be additive. Plants differ in their response to CO₂ and UV-B, they respond in general positively to elevated CO₂ and negatively to enhanced UV-B. Moreover, plant species differ in their responsiveness to CO₂ and UV-B. Therefore, even in case of additive CO₂ and UV-B effects, plant competitive relationships may change markedly under current climatic change with simultaneous enhanced atmospheric CO₂ and solar UV-B radiation.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, ENHANCEMENT, GROWTH, PHOTOSYNTHESIS, RICE

2065

Rudorff, B.F.T., C.L. Mulchi, C.S.T. Daughtry, and E.H. Lee. 1996.

Growth, radiation use efficiency, and canopy reflectance of wheat and corn grown under elevated ozone and carbon dioxide atmospheres. *Remote Sensing of Environment* 55(2):163-173.

Estimates of increases in future agricultural production in response to increases in carbon dioxide (CO₂) concentrations in the atmosphere are often based on the beneficial physiological effect of CO₂ enrichment on plant growth, especially in C-3 plants. However, these estimates fail to consider the negative impact of ozone (O-3) air pollution on crop production. Increases in tropospheric concentrations of both gases, CO₂ and O-3, have been observed over the past century, and both are predicted to continue to increase at even higher rates in the near future to levels when they may have a significant impact on agricultural production. Field studies with wheat (*Triticum aestivum* L.) in 1991 and 1992, and corn (*Zea mays* L.) in 1991 were conducted using open-top chambers to mimic atmospheric concentrations of CO₂ (similar to 500 μ mol L⁻¹ CO₂) and O-3 (similar to 40 nL L⁻¹ O-3 above ambient air [O-3] during 7h day⁻¹ 5 days week⁻¹) that are predicted to occur at the Earth surface during the first half of the 21st century. Wheat and corn (C-3 vs. C-4) produced clearly different responses to CO₂ enrichment, but similar responses to O-3 exposure. In wheat, O-3 exposure led to reduced grain yield, biomass, and radiation use efficiency (RUE, phytomass production per unit of energy received); in both years; but reduction in accumulated absorbed photosynthetically active radiation (AAPAR) was observed only in 1991. Conversely, CO₂ enrichment produced greater grain yield, dry biomass, and RUE. With CO₂ enrichment, the O-3-induced stress to wheat plants was apparently ameliorated since responses were equivalent to the control group (low O-3 and ambient CO₂) for all variables. In contrast, corn demonstrated no benefit to CO₂ enrichment for measured variables, and corn grain yield was the only parameter negatively influenced by O-3 exposure that is attributed to O-3-induced damage during the flowering process. Additionally, no treatment differences were observed for leaf area index (LAI) as determined nondestructively using the LICOR LAI-2000 Plant Canopy Analyzer. Also, treatment differences for normalized difference vegetation index (ND) were only observed for wheat plants from the high-O-3 and ambient-CO₂ treatment, at some growing stages. Otherwise, ND were not helpful for identifying damage due to O-3 fumigation or benefits due to CO₂ enrichment. Significant interactive effects of CO₂ vs. O-3 were observed only for wheat grain yield in 1991 ($p < 0.10$), indicated that the detrimental effect of O-3 air pollution was more than overcome under the CO₂-enriched environment.

KEYWORDS: BIOMASS, CHAMBERS, CO₂, FIELD, O-3, RESPONSES, VEGETATION

2066

Rudorff, B.F.T., C.L. Mulchi, P. Fenny, E.H. Lee, and R. Rowland. 1996. Wheat grain quality under enhanced tropospheric CO₂ and O-3 concentrations. *Journal of Environmental Quality* 25(6):1384-1388.

It is expected that the progressive increase of tropospheric trace gases such as CO₂ and O-3 will have a significant impact on agricultural production. The single and combined effects of CO₂ enrichment and tropospheric O-3 on grain quality characteristics in soft red winter wheat (*Triticum aestivum* L.) were examined in held studies using 3 m in diam. open-top chambers. Wheat cultivars 'Massey' (1991) and 'Saluda' (1992) were exposed to two CO₂ concentrations (350 vs. 590 μ mol CO₂ mol⁻¹; 12 h d⁻¹) in combination with two O-3 regimes (charcoal-filtered air vs. ambient air + 40 \pm 20 nmol O-3 mol⁻¹, 7 h d⁻¹ Monday to Friday) from late March until maturity in June. Grain quality characteristics investigated included: test weight, milling and baking quality, flour yield, protein content, softness equivalent, alkaline water retention capacity, and cookie diameter. In general, exposure of plants to either elevated CO₂ or weekly chronic O-3 episodes caused only small changes in grain quality. Milling and baking quality score were not significantly changed in response to treatments in both years. Flour yield

was increased by elevated CO₂ but this increase was counteracted when elevated CO₂ was combined with chronic O-3 exposure. Flour protein contents were increased by enhanced O-3 exposure and reduced by elevated CO₂. Softness equivalent was increased by 2.4% by enhanced O-3 exposure but unaffected by O-3 under elevated CO₂. Although the single effect of either CO₂ enrichment or chronic O-3 exposure had some impact on grain quality characteristic, it was noted that the combined effect of these gases was minor. It is likely that the concomitant increase of CO₂ and O-3 in the troposphere will have no significant impact on wheat grain quality.

KEYWORDS: FIELD, OPEN-TOP CHAMBERS, OZONE, RED WINTER-WHEAT, RESPONSES, VEGETATION, YIELD

2067

Rudorff, B.F.T., C.L. Mulchi, E.H. Lee, R. Rowland, and R. Pausch. 1996. Effects of enhanced O-3 and CO₂ enrichment on plant characteristics in wheat and corn. *Environmental Pollution* 94(1):53-60.

The effects of CO₂ enrichment and O-3 induced stress on wheat (*Triticum aestivum* L.) and corn (*Zea mays* L.) were studied in field experiments using open-top chambers to simulate the atmospheric concentrations of these two gases that are predicted to occur during the coming century. The experiments were conducted at Beltsville, MD, during 1991 (wheat and corn) and 1992 (wheat). Crops were grown under charcoal filtered (CF) air or ambient air +40 nL liter⁻¹ O-3 (7 h per day, 5 days per week) having ambient CO₂ concentration (350 μ mol liter⁻¹ CO₂) or +150 μ mol liter⁻¹ CO₂ (12 h per day). Averaged over O-3 treatments, the CO₂-enriched environment had a positive effect on wheat grain yield (26% in 1991 and 15% in 1992) and dry biomass (15% in 1991 and 9% in 1992). Averaged over CO₂ treatments, high O-3 exposure had a negative impact on wheat grain yield (-15% in 1991 and -11% in 1992) and drill biomass (-11% in 1991 and -9% in 1992). Averaged over CO₂ treatments, high O-3 exposure decreased corn grain yield by 9%. No significant interactive effects were observed for either crop. The results indicated that CO₂ enrichment had a beneficial effect in wheat (C-3 crop) but not in corn (C-4 crop). It is likely that the O-3-induced stress will be diminished under increased atmospheric CO₂ concentrations; however, maximal benefits in crop production in wheat in response to CO₂ enrichment will not be materialized under concomitant increases in tropospheric O-3 concentration. Copyright (C) 1996 Elsevier Science Ltd.

KEYWORDS: CHRONIC OZONE, CROP YIELD, DRY-MATTER, ELEVATED CARBON-DIOXIDE, GRAIN QUALITY, INCREASED ATMOSPHERIC CO₂, RED WINTER-WHEAT, SPRING WHEAT, TOP FIELD CHAMBERS, TRITICUM-AESTIVUM L

2068

Rudorff, B.F.T., C.L. Mulchi, E. Lee, R. Rowland, and R. Pausch. 1996. Photosynthetic characteristics in wheat exposed to elevated O-3 and CO₂. *Crop Science* 36(5):1247-1251.

Tropospheric trace gases such as CO₂ and O-3 have progressively increased over the past century and are predicted to increase to levels at which they may have a significant impact on agricultural production. The effects of CO₂ enrichment and O-3 air pollution on leaf photosynthesis (P_n) and stomatal conductance (g_s) were investigated. Two soft red winter wheat (*Triticum aestivum* L.) cultivars, Massey in 1991 and Saluda in 1992, were studied in field experiments at Beltsville, MD, by means of open-top chambers to mimic atmospheric environments predicted for the first half of the 21st century. Plants were exposed to two levels of O-3 (charcoal filtered air and ambient air + an average of 40 nmol O-3 mol⁻¹) from Monday-Friday of every week. Ozone treatments were superimposed on two CO₂ treatments (350 μ mol CO₂ mol⁻¹ and 500 μ mol CO₂ mol⁻¹). Averaged over O-3

treatments, P-n was stimulated during the early and late growing season under enriched CO₂. Averaged over CO₂ treatments, high O-3 exposure had a negative impact on P-n early in the season of 1992 and a major impact late in the season of 1991 and 1992 due to premature senescence. Decreases in g(s) occurred under the enriched CO₂ environment and to a lesser extent with high O-3. Interactive effects on P-n, and g(s) were mostly absent. It is likely that if CO₂ and O-3 concentrations continue to increase, the beneficial effect of CO₂ enrichment on P-n may be partially negated by O-3-induced stress. Conversely, damaging effects of O-3 on P-n may be compensated by elevated atmospheric CO₂.

KEYWORDS: AIR- POLLUTANTS, ATMOSPHERIC CO₂, CARBON DIOXIDE, FIELD, GAS-EXCHANGE, GROWTH, OZONE, PLANTS, RADIATION, RESPONSES

2069

Rufty, T.W., R.B. Thomas, J.D. Cure, and W.W. Cure. 1994. Growth-response of cotton to CO₂ enrichment in differing light environments. *Physiologia Plantarum* 91(3):503-509.

Experiments were conducted to examine the growth responses of cotton (*Gossypium hirsutum* L. cv. Coker 315) to CO₂ enrichment under different light regimes. Plants were exposed to 350 or 700 $\mu\text{mol l}^{-1}$ CO₂ and six light treatments differing in photosynthetic period length (8 or 16 h) and in photosynthetic photon flux density (PPFD) for 32 days of vegetative growth. Higher PPFD (1100 $\mu\text{mol m}^{-2} \text{s}^{-1}$) was provided by a combination of high intensity discharge and incandescent lamps (HID), and lower PPFD (550 $\mu\text{mol m}^{-2} \text{s}^{-1}$) was provided by fluorescent and incandescent lamps (F) or HID and incandescent lamps with shade cloth (HIDs). Growth was generally much slower with the 8-h photosynthetic periods, but the growth stimulation by CO₂ enrichment was larger than with 16-h photosynthetic periods. After 28 to 32 days of treatment, the growth enhancement with CO₂ enrichment was 152 and 78% for 8- and 16-h photosynthetic periods, respectively, under HID; 100 and 77% in F, and 77 and 56% in HIDs. The higher PPFD of HID positively influenced the CO₂ effect only at the slower growth rate in the 8-h light period. The stimulation of leaf area expansion by CO₂ enrichment was also greater with the 8-h photosynthetic period for all light sources. These results, and others on net assimilation rate, shoot to root dry weight ratios and specific leaf weights, suggest that the growth response to CO₂ enrichment with the longer photosynthetic period was depressed by limiting factors, perhaps nutritional, in the growth environment. The results also show that extensive variability in CO₂ response can occur under light intensities which are often used in growth chamber experiments.

KEYWORDS: DRY-MATTER, ELEVATED CARBON-DIOXIDE, EXPANSION, LEAVES, NITROGEN STRESS, PHOTOSYNTHETIC ACCLIMATION, SEEDLINGS, SOYBEAN PLANTS, YIELD

2070

Ruget, F., O. Bethenod, and L. Combe. 1996. Repercussions of increased atmospheric CO₂ on maize morphogenesis and growth for various temperature and radiation levels. *Maydica* 41(3):181-191.

The effect of atmospheric CO₂ enhancement on maize production was studied through four crops in two glasshouse compartments, with and without CO₂ enrichment. Development (number of organs, duration of phenological phases) was measured during cultivation and growth (dry matter production) was measured at flowering and at final harvest. The main results were as follows: The number of initiated organs (florets and leaves) was not affected by the CO₂ enrichment. According to the runs, aerial and whole plant production were significantly or not increased in the enriched compartment. The production increase was significantly different between treatments under poor radiation or high plant demand conditions. The balance between supply and demand enabled or not the

effect of CO₂ enhancement to be expressed. Among the four crops, the light conversion efficiency was significantly modified by CO₂ enrichment only in one run. The dry matter increase was not equally partitioned between the organs. It was higher in stem, husks and cob than in leaves and grains. These organs have a morphogenetically limited size (through the number of grains). This controlled the expression of the effect of CO₂ enhancement in these runs and explained why the conversion efficiency only increased in one run, which was not morphogenetically limited. These crops proved the interactions between CO₂ concentration and the other main climatic factors (temperature and radiation) and the need to know the morphogenesis in order to be able to estimate the effects of CO₂ enrichment correctly.

KEYWORDS: ACCUMULATION, CARBON-DIOXIDE ENRICHMENT, DRY-MATTER PRODUCTION, ELEVATED CO₂, PLANT-RESPONSES, SOIL-WATER, SOURCE-SINK RELATIONS, USE EFFICIENCY

2071

Runion, G.B., E.A. Curl, H.H. Rogers, P.A. Backman, R. Rodriguezkabana, and B.E. Helms. 1994. Effects of free-air CO₂ enrichment on microbial-populations in the rhizosphere and phyllosphere of cotton. *Agricultural and Forest Meteorology* 70(1-4):117-130.

Cotton (*Gossypium hirsutum* L.) plants were exposed to free-air CO₂ enriched (FACE = 550 $\mu\text{mol mol}^{-1}$) or ambient (CONTROL = 370 $\mu\text{mol mol}^{-1}$) levels of atmospheric CO₂ and to wet (100% of evapotranspiration replaced) or dry (67% of ET replaced) soil water content treatments. Foliar, soil and root samples were collected in June and August 1991 to determine the effects of elevated CO₂ on selected groups of phyllosphere and rhizosphere microorganisms. Foliage and rhizosphere soil were analyzed for bacteria and/or fungi using dilution plating. Mycorrhizal colonization of cotton roots was assessed. Root-zone soil was analyzed for populations of nematodes, microarthropods and Rhizoctonia using various extraction methods. A dehydrogenase assay for total microbial respiration and a bioassay for cotton root infecting organisms were also conducted using root-zone soil. Populations of fungi on cotton leaves varied, by genera, in response to CO₂ enrichment, but none was affected by soil water content treatments; populations of foliar bacteria were not affected by either CO₂ or soil water content treatments. In August, higher total numbers of rhizosphere fungi were found under the wet compared with the dry soil water treatment, but differences related to CO₂ were not detected. There was a trend for infestation by *Rhizoctonia solani* to be higher under FACE in the August sample, but the soil bioassay demonstrated no increase in damping-off potential. There was a significant interaction between CO₂ concentration and soil water content for populations of saprophagous nematodes; populations were different between the CO₂ levels in the dry soil treatment only, with higher numbers under FACE. Microarthropod numbers were low; however, there was a trend for Collembola populations to be higher under FACE in the August sample and more fungi were isolated from Collembola in June. Total microbial activity was higher under FACE at both sample dates. Effects of elevated atmospheric CO₂ on plant-microbe interactions could have profound influence on the productivity of agro-ecosystems, and deserve further research.

KEYWORDS: ATMOSPHERIC CO₂, CARBON DIOXIDE, COLLEMBOLA, GROWTH, NITROGEN, NODULATION

2072

Runion, G.B., J.A. Entry, S.A. Prior, R.J. Mitchell, and H.H. Rogers. 1999. Tissue chemistry and carbon allocation in seedlings of *Pinus palustris* subjected to elevated atmospheric CO₂ and water stress. *Tree Physiology* 19(4-5):329-335.

Longleaf pine (*Pinus palustris* Mill.) seedlings were grown in 45-l pots and exposed to ambient or elevated (365 or 730 $\mu\text{mol CO}_2 \text{ mol}^{-1}$) CO_2 concentration in open-top chambers for 20 months. Two water-stress treatments (target values of -0.5 or -1.5 MPa xylem pressure potential) were imposed 19 weeks after initiation of the study. At harvest, tissues (needles, stems, taproots, coarse roots, and fine roots) were analyzed for carbon (C), nitrogen (N), nonpolar extractives (fats, waxes, and oils), nonstructural carbohydrates (sugars and starch), structural components (cellulose and lignin), and tannins. The greatest dry weights and lowest N concentrations occurred in tissues of plants grown at elevated CO_2 or with adequate water. Although allocation of C fractions among tissues was generally unaffected by treatments, concentrations of the analyzed compounds were influenced by treatments in needles and taproots, but not in stems and lateral roots. Needles and taproots of plants exposed to elevated CO_2 had increased concentrations of nonstructural carbohydrates. Among plant tissues, elevated CO_2 caused reductions in structural C concentrations and foliar concentrations of fats, waxes and oils.

KEYWORDS: ARMILLARIA-OSTOYAE, CLIMATE CHANGE, DECIDUOUS TREES, DECOMPOSITION RATES, INSECT PERFORMANCE, LEAF LITTER, LONGLEAF PINE, NUTRIENT BALANCE, SOIL CARBON, USE EFFICIENCY

2073

Runion, G.B., R.J. Mitchell, T.H. Green, S.A. Prior, H.H. Rogers, and D.H. Gjerstad. 1999. Longleaf pine photosynthetic response to soil resource availability and elevated atmospheric carbon dioxide. *Journal of Environmental Quality* 28(3):880-887.

Gas exchange responses during a drought cycle were studied in longleaf pine (*Pinus palustris* Mill.) seedlings after prolonged exposure to varying levels of atmospheric CO_2 (approximate to 365 or approximate to 730 $\mu\text{mol CO}_2 \text{ mol}^{-1}$), soil N (40 or 100 $\text{kg N ha}^{-1} \text{ yr}^{-1}$), and water ("adequate" and "stressed"). Elevated atmospheric CO_2 concentration increased photosynthesis, tended to decrease stomatal conductance, and increased water-use efficiency (WUE). Although soil resource availability influenced gas exchange measurements, it generally did not affect the magnitude or direction of the response to CO_2 concentration. However, significant interactions among treatment variables were observed for plant xylem pressure potential. In seedlings grown with high N, a positive growth response to elevated atmospheric CO_2 increased whole-plant water use resulting in more severe plant water stress, despite increased leaf-level WUE; however, under low N conditions the lack of a growth response to elevated CO_2 reduced whole-plant water use, decreased water stress severity, and increased WUE. Photosynthetic response to CO_2 was greatest in the high N treatment at the beginning of the drought cycle, but diminished as water stress increased; however, plants grown with low N showed greater photosynthetic responses to CO_2 later in the drought cycle. Therefore, plant gas exchange rates interact with growth response in determining the severity of water stress under drought and, thus, the ability of elevated atmospheric CO_2 to ameliorate the effects of drought and allow plants to maintain increased rates of photosynthesis may be influenced by the availability of other resources, such as N and water.

KEYWORDS: CO_2 - ENRICHMENT, DROUGHT STRESS, FIELD, GAS-EXCHANGE, GROWTH, LOBLOLLY-PINE, NITROGEN, PLANT-RESPONSES, SEEDLINGS, WATER-USE EFFICIENCY

2074

Running, S.W., D.D. Baldocchi, D.P. Turner, S.T. Gower, P.S. Bakwin, and K.A. Hibbard. 1999. A global terrestrial monitoring network integrating tower fluxes, flask sampling, ecosystem modeling and EOS satellite data. *Remote Sensing of Environment* 70(1):108-127.

Accurate monitoring of global scale changes in the terrestrial biosphere has become acutely important as the scope of human impacts on biological systems and atmospheric chemistry grows. For example, the Kyoto Protocol of 1997 signals some of the dramatic socioeconomic and political decisions that may lie ahead concerning CO_2 emissions and global carbon cycle impacts. These decisions will rely heavily on accurate measures of global biospheric changes (Schimel 1998; IGBP TCWG, 1998). An array of national and international programs have inaugurated global satellite observations, critical field measurements of carbon and water fluxes, and global model development for the purposes of beginning to monitor the biosphere. The detection by these programs of interannual variability of ecosystem fluxes and of longer term trends will permit early indication of fundamental biospheric changes which might otherwise go undetected until major biome conversion begins. This article describes a blueprint for more comprehensive coordination of the various flux measurement and modeling activities into a global terrestrial monitoring network that will have direct relevance to the political decision making of global change. (C) Elsevier Science Inc., 1999.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATE CHANGE, CO_2 , EDDY-CORRELATION, EXCHANGE, FOREST, NET PRIMARY PRODUCTION, SEASONAL-VARIATION, SPATIAL-RESOLUTION, WATER-VAPOR

2075

Rustad, L.E., and I.J. Fernandez. 1998. Experimental soil warming effects on CO_2 and CH_4 flux from a low elevation spruce-fir forest soil in Maine, USA. *Global Change Biology* 4(6):597-605.

The effect of soil warming on CO_2 and CH_4 flux from a spruce-fir forest soil was evaluated at the Howland Integrated Forest Study site in Maine, USA from 1993 to 1995. Elevated soil temperatures (similar to 5 degrees C) were maintained during the snow-free season (May-November) in replicated 15 x 15-m plots using electric cables buried 1-2 cm below the soil surface; replicated unheated plots served as the control. CO_2 evolution from the soil surface and soil air CO_2 concentrations both showed clear seasonal trends and significant ($P < 0.0001$) positive exponential relationships with soil temperature. Soil warming caused a 25-40% increase in CO_2 flux from the heated plots compared to the controls. No significant differences were observed between heated and control plot soil air CO_2 concentrations which we attribute to rapid equilibration with the atmosphere in the O horizon and minimal treatment effects in the B horizon. Methane fluxes were highly variable and showed no consistent trends with treatment.

KEYWORDS: BALANCE, CLIMATE, FLOOR, METHANE, PATTERNS, RESPIRATION, TEMPERATURE, TRACE GAS FLUXES

2076

Rusterholz, H.P., and A. Erhardt. 1998. Effects of elevated CO_2 on flowering phenology and nectar production of nectar plants important for butterflies of calcareous grasslands. *Oecologia* 113(3):341-349.

Effects of elevated CO_2 on flowering phenology and nectar production were investigated in *Trifolium pratense*, *Lotus corniculatus*, *Scabiosa columbaria*, *Centaurea jacea* and *Betonica officinalis*, which are all important nectar plants for butterflies. In glasshouse experiments, juvenile plants were exposed to ambient (350 $\mu\text{mol l}^{-1}$) and elevated (660 $\mu\text{mol l}^{-1}$) CO_2 concentrations for 60-80 days. Elevated CO_2 significantly enhanced the development of flower buds in *C. jacea*. *B. officinalis* flowered earlier and *L. corniculatus* produced more flowers under elevated CO_2 . In contrast, the number of flowers decreased in *T. pratense*. The amount of nectar per flower was not affected by elevated CO_2 in the tested legumes (*T. pratense* and *L. corniculatus*), but was significantly reduced (!) in the other forbs. Elevated CO_2 did not

significantly affect nectar sugar concentration and composition. However, *S. columbaria* and *C. jacea* produced significantly less total sugar under elevated CO₂. The nectar amino acid concentration remained unaffected in all investigated plant species, whereas the total of amino acids produced per flower was reduced in all non-legumes. In addition, the amino acid composition changed significantly in all investigated species except for *C. jacea*. The observed effects are unexpected and are a potential threat to flower visitors such as most butterflies which have no alternative food resources to nectar. Changes in nectar production due to elevated CO₂ could also have generally detrimental effects on the interactions of flowers and their pollinators.

KEYWORDS: ADULT DIET, AMINO-ACIDS, ATMOSPHERIC CARBON-DIOXIDE, CHROMATOGRAPHY, ENRICHMENT, GROWTH, LEPIDOPTERA, LIQUIDAMBAR-STYRACIFLUA, PINUS-TAEDA SEEDLINGS, RESPONSES

2077

Ryan, M.G. 1991. Effects of climate change on plant respiration. *Ecological Applications* 1(2):157-167.

Plant respiration is a large, environmentally sensitive component of the ecosystem carbon balance, and net ecosystem carbon flux will change as the balance between photosynthesis and respiration changes. Partitioning respiration into the functional components of construction, maintenance, and ion uptake will aid the estimation of plant respiration for ecosystems. Maintenance respiration is the component most sensitive to changes in temperature, CO₂, protein concentration and turnover, water stress, and atmospheric pollutants. For a wide variety of plant tissues, maintenance respiration, corrected for temperature, appears to be linearly related to Kjeldahl nitrogen content of live tissue. Total and maintenance respiration may decline under CO₂ enrichment, but the mechanism, independence from changes in protein content, and acclimation are unknown. Response of respiration to temperature can be modelled as a Q₁₀ relationship, if corrections for bias arising from daily and annual temperature amplitude are applied. Occurrence and control of the cyanide-resistant respiratory pathway and acclimation of respiration rates to different climates are poorly understood, but may substantially affect the reliability of model estimates of plant respiration.

KEYWORDS: CO₂, CYANIDE- RESISTANT, DARK RESPIRATION, ELEVATED CARBON-DIOXIDE, GRAIN-SORGHUM, GROWTH, LOLIUM-MULTIFLORUM, MAINTENANCE RESPIRATION, ROOT RESPIRATION, WHOLE PLANTS

2078

Rygielwicz, P.T., and C.P. Andersen. 1994. Mycorrhizae alter quality and quantity of carbon allocated below ground. *Nature* 369(6475):58-60.

PLANTS and soils are a critically important element in the global carbon-energy equation. It is estimated that in forest ecosystems over two-thirds of the carbon is contained in soils and peat deposits(1). Despite the importance of forest soils in the global carbon cycle, fluxes of carbon associated with fundamental processes and soil functional groups are inadequately quantified, limiting our understanding of carbon movement and sequestration in soils. We report here the direct measurement of carbon id and through all major pools of a mycorrhizal (fungus-root) coniferous seedling (a complete carbon budget). The mycorrhizal symbiont reduces overall retention of carbon in the plant-fungus symbiosis by increasing carbon in roots and below-ground respiration and reducing its retention and release above ground. Below ground, mycorrhizal plants shifted allocation of carbon to pools that are rapidly turned over, primarily to fine roots and fungal hyphae, and host root and fungal respiration. Mycorrhizae alter the size of below-ground carbon pools, the quality and, therefore, the retention time of carbon

below ground. Our data indicate that if elevated atmospheric CO₂ and altered climate stressors alter mycorrhizal colonization in forests, the role of forests in sequestering carbon could be altered.

KEYWORDS: CO₂, FLOW, HYPHAE, ROOTS, SEEDLINGS, SOIL

2079

Rygielwicz, P.T., M.G. Johnson, L.M. Ganio, D.T. Tingey, and M.J. Storm. 1997. Lifetime and temporal occurrence of ectomycorrhizae on ponderosa pine (*Pinus ponderosa* Laws) seedlings grown under varied atmospheric CO₂ and nitrogen levels. *Plant and Soil* 189(2):275-287.

Climate change (elevated atmospheric CO₂, and altered air temperatures, precipitation amounts and seasonal patterns) may affect ecosystem processes by altering carbon allocation in plants, and carbon flux from plants to soil. Mycorrhizal fungi, as carbon sinks, are among the first soil biota to receive carbon from plants, and thereby influence carbon release from plants to soil. One step in this carbon release is via fine root and mycorrhizal turnover. It is necessary to know the lifetime and temporal occurrence of roots and mycorrhizae to determine the capacity of the soil ecosystem to sequester carbon assimilated aboveground. In this study, ponderosa pine (*Pinus ponderosa* Laws) seedlings were grown under three levels of atmospheric CO₂ (ambient, 525 and 700 $\mu\text{mol CO}_2 \text{ mol}^{-1}$) and three levels of annual nitrogen additions (0, 100 and 200 kg N ha⁻¹) in open-top chambers. At a two-month frequency during 18 months, we observed ectomycorrhizal root tips observed using minirhizotron tubes and camera. The numbers of new mycorrhizal root tips, the numbers of tips that disappeared between two consecutive recording events, and the standing crop of tips at each event were determined. There were more mycorrhizal tips of all three types seen during the summer compared with other times of the year. When only the standing crop of mycorrhizal tips was considered, effects of the CO₂ and N addition treatments on carbon allocation to mycorrhizal tips was weakly evident. However, when the three types of tips were considered collectively, tips numbers flux of carbon through mycorrhizae was greatest in the: (1) high CO₂ treatment compared with the other CO₂ treatments, and (2) intermediate N addition treatment compared with the other N addition treatments. A survival analysis on the entire 18 month cohort of tips was done to calculate the median lifetime of the mycorrhizal root tips. Average median lifetime of the mycorrhizal tips was 139 days and was not affected by nitrogen and CO₂ treatments.

KEYWORDS: CARBON, COMPENSATORY INCREASES, DOUGLAS-FIR STANDS, ELEVATED CO₂, FINE ROOTS, FOREST, MYCORRHIZAL COLONIZATION, QUERCUS-ALBA, SEMINAL ROOT-SYSTEM, SOIL RESPIRATION

2080

Ryle, G.J.A., and C.E. Powell. 1992. The influence of elevated CO₂ and temperature on biomass production of continuously defoliated white clover. *Plant, Cell and Environment* 15(5):593-599.

Clonal plants of white clover (*Trifolium repens* L.), grown singly in pots of Perlite and solely dependent for nitrogen on root nodule N₂ fixation, were maintained in controlled environments which provided four environments: 18/13-degrees-C day/night temperature at 340 and 680- $\mu\text{mol mol}^{-1}$ CO₂ and 20.5/15.5-degrees-C day/night temperature at 340 and 680- $\mu\text{mol mol}^{-1}$ CO₂. The daylength was 12h and the photon flux density 500 \pm 25- $\mu\text{mol m}^{-2} \text{ s}^{-1}$ (PPFD). All plants were defoliated for about 80d, nominally every alternate day, to leave the youngest expanded leaf intact on 50% of stolons, plus expanding leaves (simulated grazing). Elevated CO₂ increased the yield of biomass removed at defoliation by a constant 45% during the second 40d of the experiment and by a varying amount in the first half of the experiment. Elevated temperature had little effect on biomass yield. Nitrogen, as a

proportion of the harvested biomass, was only fractionally affected by elevated CO₂ or temperature. In contrast, N₂ fixation increased in concert with the promoting effect of elevated CO₂ on biomass production. The increased yield of biomass harvested in 680 $\mu\text{mol mol}^{-1}$ CO₂ was primarily due to the early development and continued maintenance of more stolons. However, the stolons of plants grown in elevated CO₂ also developed leaves which were heavier and slightly larger in area than their counterparts in ambient CO₂. The conclusion is that, when white clover plants are maintained at constant mass by simulated grazing, they continue to respond to elevated CO₂ in terms of a sustained increase in biomass production.

KEYWORDS: CARBONDIOXIDE, ENRICHMENT, ENVIRONMENTS, GROWTH, PHOTOSYNTHESIS, YIELD

2081

Ryle, G.J.A., C.E. Powell, and I.A. Davidson. 1992. Growth of white clover, dependent on n₂ fixation, in elevated co₂ and temperature. *Annals of Botany* 70(3):221-228.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, NITROGEN, PHOTOSYNTHESIS, PLANT GROWTH, RESPIRATION, STARCH

2082

Ryle, G.J.A., C.E. Powell, and V. Tewson. 1992. Effect of elevated co₂ on the photosynthesis, respiration and growth of perennial ryegrass. *Journal of Experimental Botany* 43(251):811-818.

Single, seed-grown plants of ryegrass (*Lolium perenne* L. cv. Melle) were grown for 49 d from the early seedling stage in growth cabinets at a day/night temperature of 20/15-degrees-C, with a 12 h photoperiod, and a CO₂ concentration of either 340 or 680- $\mu\text{mol l}^{-1}$ CO₂. Following complete acclimation to the environmental regimes, leaf and whole plant CO₂ effluxes and influxes were measured using infra-red gas analysis techniques. Elevated CO₂ increased rates of photosynthesis of young, fully expanded leaves by 35-46% and of whole plants by more than 50%. For both leaves and whole plants acclimation to 680- $\mu\text{mol l}^{-1}$ CO₂ reduced rates of photosynthesis in both CO₂ regimes, compared with plants acclimated to 340- $\mu\text{mol l}^{-1}$. There was no significant effect of CO₂ regime on respiration rates of either leaves or whole plants, although leaves developed in elevated CO₂ exhibited generally lower rates than those developed in 340- $\mu\text{mol l}^{-1}$ CO₂. Initially the seedling plants in elevated CO₂ grew faster than their counterparts in 340- $\mu\text{mol l}^{-1}$ CO₂, but this effect quickly petered out and final plant weights differed by only c. 10%. Since the total area of expanded and unexpanded laminae was unaffected by CO₂ regime, specific leaf area was persistently 13-40% lower in elevated CO₂ while, similarly, root/shoot ratio was also reduced throughout the experiment. Elevated CO₂ reduced tissue nitrogen contents of expanded leaves, but had no effect on the nitrogen contents of unexpanded leaves, sheaths or roots. The lack of a pronounced effect of elevated CO₂ on plant growth was primarily due to the fact that CO₂ concentration did not influence tiller (branch) numbers. In the absence of an effect on tiller numbers, any possible weight increment was restricted to the c. 2.5 leaves of each tiller. The reason for the lack of an effect on tillering is not known.

KEYWORDS: CARBON-DIOXIDE CONCENTRATION, ENRICHMENT, LIGHT, LOLIUM, NITROGEN, PLANTS, RESPONSES

2083

Ryle, G.J.A., and J. Stanley. 1992. Effect of elevated co₂ on stomatal size and distribution in perennial ryegrass. *Annals of Botany* 69(6):563-565.

KEYWORDS: ENRICHMENT, GROWTH

2084

Ryle, G.J.A., J. Woledge, V. Tewson, and C.E. Powell. 1992. Influence of elevated co₂ and temperature on the photosynthesis and respiration of white clover dependent on n₂ fixation. *Annals of Botany* 70(3):213-220.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ENRICHMENT, GAS-EXCHANGE, GRASS, LEAVES, NITROGEN, PLANT GROWTH, SHORT- TERM

2085

Sa, T., and D.W. Israel. 1997. Effect of phosphorus deficiency on response of symbiotic N-2 fixation of soybean to atmospheric CO₂ enrichment. *Plant Physiology* 114(3):484.

2086

Sa, T.N., and D.W. Israel. 1998. Phosphorus-deficiency effects on response of symbiotic N-2 fixation and carbohydrate status in soybean to atmospheric CO₂ enrichment. *Journal of Plant Nutrition* 21(10):2207-2218.

The impact of phosphorus (P) deficiency on response of symbiotic N-2 fixation and carbohydrate accumulation in soybean (*Glycine max* [L.] Merr.) to atmospheric CO₂ enrichment was examined. Plants inoculated with *Bradyrhizobium japonicum* MN 110 were grown in growth chambers with controlled atmospheres of 400 and 800 $\mu\text{mol L}^{-1}$ CO₂ and supplied either 1.0 mM-P (P-sufficient) or 0.05 mM-P (P-deficient) nitrogen (N)-free nutrient solution. When plants were supplied with sufficient P, CO₂ enrichment significantly increased whole plant dry mass (83%), nodule mass (67%), total nitrogenase activity (58%), and N (35%) and P (47%) accumulation at 35 days after transplanting (DAT). Under sufficient P supply, CO₂ enrichment significantly increased starch concentrations in nodules compared to the normal atmospheric CO₂ treatment. Under normal CO₂ levels (400 $\mu\text{mol L}^{-1}$) nonstructural carbohydrate concentration (starch plus soluble sugar) was significantly higher in leaves of P-deficient plants than in leaves of P-sufficient plants in which nonstructural carbohydrate concentration exhibited a strong diurnal pattern. Under deficient P supply whole plant dry mass, symbiotic N-2-fixation parameters, and N and P accumulation were not enhanced by atmospheric CO₂ enrichment. Phosphorus deficiency decreased nonstructural carbohydrate accumulation in nodules at the end of a 10-day period in which functional activity was developing by 86% relative to P-sufficient controls. While P deficiency elicited significant increases in the nonstructural carbohydrate concentration in leaves, it caused significant decreases in the nonstructural carbohydrate concentration in nodules over the diurnal cycle from 30 to 31 DAT. Collectively, these results indicate that the lack of a symbiotic N-2-fixation response to atmospheric CO₂ enrichment by P-deficient plants may be related to the decreased carbohydrate status of nodules.

KEYWORDS: ELEVATED CARBON-DIOXIDE, GLYCINE-MAX, GROWTH, NUTRITION, PLANTS, SEED YIELD, TOTAL NITROGEN

2087

Saarinen, T. 1998. Internal C : N balance and biomass partitioning of *Carex rostrata* grown at three levels of nitrogen supply. *Canadian Journal of Botany-Revue Canadienne De Botanique* 76(5):762-768.

The long-term effects of high nitrogen supply on the growth and partitioning of biomass in a common sedge species, *Carex rostrata* Stokes, were studied in a greenhouse experiment. Special attention was paid to free amino acids and soluble sugars, representing biochemically

available fractions of nitrogen and carbon, respectively, in the tissues of Carer. Plants were grown in peat in buckets, and nitrogen was added as ammonium nitrate (2, 5, and 10 g N m⁻² year⁻¹) five times during two growing seasons. Changes in biomass allocation patterns became evident towards the end of the second growing season. The biomass of shoots was highest in the high-N treatment, resulting in a high ratio of aboveground to belowground biomass. The high biomass of shoots was due to both the high density of current-year shoots and later senescence in the high-N treatment. No differences were observed in the belowground biomasses. Changes in allocation patterns were accompanied by changes in the soluble fractions of carbon and nitrogen. The concentration of free amino acids (FAA) was significantly higher (both shoots and roots) and the concentration of total nonstructural carbohydrates (TNC) lower (roots only) in the high-N treatment. The concentration of total nitrogen also increased with increasing supply of nitrogen. The results indicate that a high long-term supply of nitrogen may shift the internal carbon to nitrogen balance of Carer towards higher availability of nitrogen. Compared with the carbon to nitrogen ratio, the TNC:FAA ratio seems to be a better indicator of the internal carbon to nitrogen balance. A low TNC:FAA ratio may enhance the allocation of biomass to shoots and also increase the density of shoots.

KEYWORDS: ALLOCATION PATTERNS, ATMOSPHERIC CO₂ ENRICHMENT, ELEVATED CO₂, FLOATING FENS, FUNCTIONAL EQUILIBRIUM, MINERAL NUTRITION, ROOT, SEASONAL ALLOCATION, SHOOT, VASCULAR PLANTS

2088

Saarnio, S., J. Alm, P.J. Martikainen, and J. Silvola. 1998. Effects of raised CO₂ on potential CH₄ production and oxidation in, and CH₄ emission from, a boreal mire. *Journal of Ecology* 86(2):261-268.

1 In a glasshouse experiment we studied the effect of raised CO₂ concentration (720 p.p.m.) on CH₄ emission at natural boreal peat temperatures using intact cores of boreal peat with living vascular plants and Sphagnum mosses. After the end of the growing season half of the cores were kept unnaturally warm (17-20 degrees C). The potential for CH₄ production and oxidation was measured at the end of the emission experiment. 2 The vascular cores ('Sedge') consisted of a moss layer with sedges, and the moss cores ('Sphagnum') of Sphagnum mosses (some sedge seedlings were removed by cutting). Methane efflux was 6-12 times higher from the Sedge cores than from the Sphagnum cores. The release of CH₄ from Sedge cores increased with increasing temperature of the peat and decreased with decreasing temperature. Methane efflux from Sphagnum cores was quite stable independent of the peat temperatures. 3 In both Sedge and Sphagnum samples, CO₂ treatment doubled the potential CH₄ production but had no effect on the potential CH₄ oxidation. A raised concentration of CO₂ increased CH₄ efflux weakly and only at the highest peat temperatures (17-20 degrees C). 4 The results suggest that in cool regions, such as boreal wetlands, temperature would restrict decomposition of the extra substrates probably derived from enhanced primary production of mire vegetation under raised CO₂ concentrations, and would thus retard any consequent increase in CH₄ emission.

KEYWORDS: CARBON DIOXIDE, CLIMATIC CHANGE, ENRICHMENT, FEEDBACK, METHANE FLUX, PEATLANDS, PHOTOSYNTHESIS, PLANT-ROOTS, TUNDRA, VEGETATION

2089

Saarnio, S., and J. Silvola. 1999. Effects of increased CO₂ and N on CH₄ efflux from a boreal mire: a growth chamber experiment. *Oecologia* 119(3):349-356.

Increases in the supply of atmospheric CO₂ and N are expected to alter the carbon cycle, including CH₄ emissions, in boreal peatlands. These

effects were studied in a glasshouse experiment with peat monoliths cored from an oligotrophic pine fen. The cores with living plants were kept in 720 ppm(v) and 360 ppm(v) CO₂ atmospheres for about 6 months under imitated natural temperature cycle. Fertilisation with NH₄NO₃ (3 g m⁻² for 25 weeks) was applied to 18 of the 36 monoliths. The rate of CH₄ flux was non-linearly dependent on the number of Eriophorum vaginatum shoots growing in the monoliths, probably due to the gas transport properties of the aerenchyma. The average CH₄ efflux rate, standardised by the number of shoots, was increased by a maximum of 10-20% in response to the raised CO₂ level. In the raised-NH₄NO₃ treatment, the increase in CH₄ release was lower. The effect of combined CO₂ + NH₄NO₃ on CH₄ release was negligible and even lower than in the single treatments. Both potential CH₄ production and oxidation rates at 5, 15 and 25 degrees C were higher near the surface than at the bottom of the core. As expected, the rates clearly depended on the incubation temperature, but the different treatments did not cause any consistent differences in either CH₄ production or oxidation. The determination of potential CH₄ production and oxidation in the laboratory is evidently too crude a method of differentiating substrate-induced differences in CH₄ production and oxidation in vivo. These results indicate that an increase in atmospheric CO₂ or N supply alone, at least in the short term, slightly enhances CH₄ effluxes from boreal peatlands; but together their effect may even be restrictive.

KEYWORDS: BIOMASS ALLOCATION, CARBON DIOXIDE, ELEVATED ATMOSPHERIC CO₂, FOREST SOILS, LEAF LITTER, LOLIUM-PERENNE, METHANE EMISSION, NITROGEN-FERTILIZATION, OLIGOTROPHIC PINE FEN, TUSsock TUNDRA

2090

Saccardy, K., B. Pineau, O. Roche, and G. Cornic. 1998. Photochemical efficiency of Photosystem II and xanthophyll cycle components in Zea mays leaves exposed to water stress and high light. *Photosynthesis Research* 56(1):57-66.

The effects of two light treatments (photosynthetically active photon flux density of either 650 or 1950 $\mu\text{mol m}^{-2} \text{s}^{-1}$) on the photochemical efficiency of Photosystem II (PS II) (measured as variable to maximum fluorescence ratio) and on the xanthophyll cycle components was studied in wilted Zea mays leaves. For comparison, these parameters were followed under the same light conditions in well-hydrated leaves maintained either in normal or CO₂-free air. The net CO₂ assimilation of dehydrated leaves declined rapidly as their relative water content (RWC) decreased from 100 to 60% while the PS II efficiency measured after a prolonged dark period of 16 h declined only when RWC leaves was lower than 60%. Furthermore, drought caused an increase in the pool size of the xanthophyll cycle pigments and the presence of a sustained elevated level of zeaxanthin and antheraxanthin at the end of the long dark period. The leaf water deficit enhanced the sensitivity of PS II efficiency to light exposure. During illumination, strong inhibition of PS II efficiency and large violaxanthin deepoxidation was observed in wilted leaves even under moderate photon flux density compared to control leaves in the same conditions. After 2 h of darkness following the light treatment, the PS II efficiency that is dependent on the previous PPFD, decreased with leaf water deficit. Moreover, zeaxanthin epoxidation led to an accumulation of antheraxanthin in dehydrated leaves. All these drought effects on PS II efficiency and xanthophyll cycle components were also obtained in well-hydrated leaves by short-term CO₂ deprivation during illumination. We conclude that the increased susceptibility of PS II efficiency to light in wilted maize leaves is mainly explained by the decrease of CO₂ availability and the resulting low net CO₂ assimilation.

KEYWORDS: CHLOROPHYLL-A FLUORESCENCE, COTTON LEAVES, DELTA, DROUGHT STRESS, ENERGY, EXCESS LIGHT, PHOTOSYNTHETIC REACTIONS, QUANTUM YIELD,

2091

Sadowsky, M.J., and M. Schortemeyer. 1997. Soil microbial responses to increased concentrations of atmospheric CO₂. *Global Change Biology* 3(3):217-224.

Terrestrial ecosystems respond to an increased concentration of atmospheric CO₂. While elevated atmospheric CO₂ has been shown to alter plant growth and productivity, it also affects ecosystem structure and function by changing below-ground processes. Knowledge of how soil microbiota respond to elevated atmospheric CO₂ is of paramount importance for understanding global carbon and nutrient cycling and for predicting changes at the ecosystem-level. An increase in the atmospheric CO₂ concentration not only alters the weight, length, and architecture of plant roots, but also affects the biotic and abiotic environment of the root system. Since the concentration of CO₂ in soil is already 10-50 times higher than that in the atmosphere, it is unlikely that increasing atmospheric CO₂ will directly influence the rhizosphere. Rather, it is more likely that elevated atmospheric CO₂ will affect the microbe-soil-plant root system indirectly by increasing root growth and rhizodeposition rates, and decreasing soil water deficit. Consequently, the increased amounts and altered composition of rhizosphere-released materials will have the potential to alter both population and community structure, and activity of soil- and rhizosphere-associated microorganisms. This occurrence could in turn affect plant health and productivity and plant community structure. This review covers current knowledge about the response of soil microbes to elevated concentrations of atmospheric CO₂.

KEYWORDS: *BOUTELOUA-GRACILIS, CROP RESPONSES, ELEVATED CARBON-DIOXIDE, ENRICHMENT, LOLIUM-PERENNE, MYCORRHIZAL COLONIZATION, PLANT-RESPONSES, RHIZOSPHERE, SEEDLING GROWTH, TALLGRASS PRAIRIE*

2092

Saebo, A., T. Krekling, and M. Appelgren. 1995. Light quality affects photosynthesis and leaf anatomy of birch plantlets in-vitro. *Plant Cell Tissue and Organ Culture* 41(2):177-185.

Cultures in vitro of *Betula pendula* Roth were subjected to light of different spectral qualities. Photosynthetic capacity was highest when the plantlets were exposed to blue light (max recorded photosynthesis, 82 $\mu\text{mol CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$) and lowest when irradiated with light high in red and/or far-red wave lengths (max recorded photosynthesis, 40 $\mu\text{mol CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$). Highest chlorophyll content (2.2 mg dm^{-2} leaf area) was found in cultures irradiated with blue light, which also enhanced the leaf area. Morphometric analysis of light micrographs showed that the epidermal cell areas were largest in plantlets subjected to blue light and smallest in those subjected to red light. Morphometric analysis of electron micrographs of palisade cells, showed that the functional chloroplast area was largest in chloroplasts of leaves subjected to blue light and smallest in those exposed to red light. We suggest that light quality affects photosynthesis both through effects on the composition of the photosynthetic apparatus and on translocation of carbohydrates from chloroplasts.

KEYWORDS: *BLUE, CULTURED INVITRO, FLUENCE RATE, GROWTH, PHYTOCHROME, PIGMENTS, RED*

2093

Saebo, A., and L.M. Mortensen. 1995. Growth and regrowth of phleum-pratense, lolium-perenne, trifolium-repens and trifolium-pratense at normal and elevated co₂ concentration. *Agriculture Ecosystems & Environment* 55(1):29-35.

The effect of elevated CO₂ concentration (680 \pm 52 $\mu\text{mol mol}^{-1}$) on growth of three cultivars of *Phleum pratense*, two of *Lolium perenne* and one of *Trifolium repens* and *Trifolium pratense* each, was studied during one growth season including three harvests. The study was performed in ten 9 m² field chamber units in a cool maritime climate under long days (15-18 h), on the southwest coast of Norway (59 degrees N, 6 degrees E). Tillering in *P. pratense* and *L. perenne* was not significantly affected in the first harvest (June/July), but was increased by 30% in the third harvest (September) in response to elevated CO₂ concentrations. The plant height was reduced by 16-24% in *P. pratense* and by 25-29% in *L. perenne* at high CO₂. The dry weight yield of the two grass species was negatively affected by elevated CO₂ in the two first harvests, however, no effect was found in the last harvest. The total harvestable dry matter was decreased by 18% in *P. pratense* and 13% in *L. perenne*. The dry matter of the stubble was increased at elevated CO₂, by 18% in *P. pratense* and 26% in *L. perenne*, leaving more of the yield in the meadow after harvest. Raising the CO₂ concentration increased the dry weight by 30% in both clover species. The results are discussed in relation to the climatic conditions during the season.

KEYWORDS: *ATMOSPHERIC CO2, CARBON DIOXIDE, DIFFERENT IRRADIANCES, ENRICHMENT, NITROGEN, TEMPERATURE, WHEAT, YIELD*

2094

Saebo, A., and L.M. Mortensen. 1996. Growth, morphology and yield of wheat, barley and oats grown at elevated atmospheric CO₂ concentration in a cool, maritime climate. *Agriculture Ecosystems & Environment* 57(1):9-15.

The effects of elevated CO₂ concentration on the growth, yield and quality of spring wheat (*Triticum aestivum* L., cv. 'Sport'), barley (*Hordeum vulgare*, cv. 'Thule') and oats (*Avena sativa*, cv. 'Kapp') were studied. The study was performed from 20 April to 24 August in ten field chamber units each of 9 m² in a cool (12.6 degrees C) maritime climate under long days (14.6-18.1 h), on the southwest coast of Norway (59 degrees N, 6 degrees E). The total biomass increased at high CO₂ concentration, by 11% and 20% in wheat and barley, respectively. The proportion of small grains increased by 6% in wheat and 26% in barley, but the total grain yield was not affected. The weight of chaff increased by 9% and 19% in wheat and barley, respectively. Plant height was significantly reduced during the growing season at elevated CO₂, by 8-19% in barley and by 9-25% in oats until 6 July when no significant difference in height was found. After 6 July, barley plants at elevated CO₂ were significantly taller than at ambient CO₂ concentration and oats were not affected. Elongation in wheat was not affected by CO₂ concentration at any time in the growing season. No difference in developmental rate could be detected between plants at normal and elevated CO₂ concentrations. The protein content of the grain decreased by 8% in barley, but was not significantly affected in the other species.

KEYWORDS: *AIR- TEMPERATURE, AMBIENT, CARBON DIOXIDE, ENRICHMENT, INHIBITION, LEAVES*

2095

Saebo, A., and L.M. Mortensen. 1996. The influence of elevated CO₂ concentration on growth of seven grasses and one clover species in a cool maritime climate. *Acta Agriculturae Scandinavica Section B-Soil and Plant Science* 46(1):49-54.

The effect of elevated CO₂ concentration on the growth of eight common species and cultivars in Norwegian meadows-*Festuca pratensis* "Salten" and "Fure", *Festuca rubra* "Koket" and "Leik", *Festuca arundinaceae* "Vantage" *Festuca duruiscula* "Barfina", *Poa pratensis* "Lavang", *Agrostis capillaris* "Aros", *Dactylis glomerata* "Apelsvoll", and *Trifolium repens* "Grasslands Huia"-was studied during 11 weeks

(April 26-early July). The study was performed in ten 9 m(2) large field chamber units in a cool (11.3 degrees C) maritime climate under long days (15.1-18.1 h), on the south-west coast of Norway (59 degrees N, 6 degrees E). The different species responded differently to elevated CO₂ with respect to tillering, which was enhanced in *A. capillaris* (81%), *D. glomerata* (23%) and *F. pratensis* (36%), but was not significantly affected in the other species. The sward length was significantly decreased by high CO₂ concentration, by 20% in *P. pratensis*, 36% in *A. capillaris*, 29% in *D. glomerata*, 26% in *F. duriscula*, 36% in *F. pratensis* and 16% in *F. rubra*, but was not affected in *F. arundinacea*, *F. pratensis* "Salten" and *T. repens*. The dry matter was decreased at elevated CO₂ concentration in *A. capillaris* (14%), increased in *F. rubra* (10%) and not significantly affected in the other plants. The results are discussed in relation to climate and interspecific responses.

KEYWORDS: AIR-TEMPERATURE, AMBIENT, ATMOSPHERIC CO₂, CARBON DIOXIDE, ENRICHMENT, NITROGEN, ORANGE TREE LEAVES, PHOSPHORUS, WHEAT, YIELD

2096

Saebo, A., and L.M. Mortensen. 1998. Influence of elevated atmospheric CO₂ concentration on common weeds in Scandinavian agriculture. *Acta Agriculturae Scandinavica Section B-Soil and Plant Science* 48(3):138-143.

This study investigated the influence of elevated CO₂ on three perennial weed species (*Achillea millefolium*, *Leontodon autumnalis* and *Rumex acetosa*) and seven annual species (*Chenopodium album*, *Matricaria matricarioides*, *Poa annua*, *Polygonum persicaria*, *Senecio vulgaris*, *Spergula arvensis* and *Stellaria media*). The study was carried out during the period 3 May to 5 August in ten field chamber units of 9 m(2) in a cool (12.6 degrees C) maritime climate under long days (15.8-18.1 h day(-1)) on the south-west coast of Norway (59 degrees N, 6 degrees E). Dry weights of the seven annual species were not significantly affected by the CO₂ concentration. Of the three perennial species, *L. autumnalis* increased in dry weight by 27% and *A. millefolium* by 19% at elevated compared with ambient CO₂ concentration. Plant height increased by 8% in *L. autumnalis* and decreased by 12 and 10% in *M. matricarioides* and *P. annua*, respectively. Leaf size increased by 32% and specific leaf area decreased by 23% in *P. persicaria* at elevated CO₂, while the other species were unaffected. The results are discussed in relation to competition between species and the influence of climate on the CO₂ responses.

KEYWORDS: AIR-TEMPERATURE, AMBIENT, CARBON DIOXIDE, COOL, ENRICHMENT, GROWTH, MARITIME CLIMATE, NITROGEN, WHEAT, YIELD

2097

Saetersdal, M., and H.J.B. Birks. 1997. A comparative ecological study of Norwegian mountain plants in relation to possible future climatic change. *Journal of Biogeography* 24(2):127-152.

Mountain plants constitute an important part of the Norwegian flora. They are also believed to be the plant group in Norway most threatened by the expected climatic warming due to an enhanced greenhouse effect in the near future. In this study the distributions of 107 mountain Norwegian vascular plants were modelled in relation to present-day climate using Gaussian legit regression. Most species are found to have a surprisingly broad amplitude to mean July and January temperatures, suggesting that a 2 degrees C increase in summer temperature and 4 degrees C increase in winter temperature (as expected with a 2 x CO₂ increase) may not have a dramatic direct effect on most of the species investigated. A comparative study between estimated July and January temperature optima and tolerances and other ecological attributes such as habitat characteristics, dispersal mechanisms, range sizes and other

climatic optima and tolerances was done using multivariate analysis. The results suggest that species most vulnerable to climatic warming, namely the species with narrow July and January temperature tolerances, are characterized by small range sizes and small population sizes, i.e. they are nationally rare species. Furthermore, these vulnerable species are found in all habitats along the major moisture gradient in alpine vegetation. A classification of the species into Rabinowitz's seven forms of rarity confirms that the species most vulnerable to climatic warming are characterized by being habitat specialists with a small geographic range size.

KEYWORDS: ABUNDANCE, ENVIRONMENTAL-CHANGE, FALLOPIA-JAPONICA, GRADIENT ANALYSIS, GROWTH, MODEL, NUMERICAL-ANALYSIS, PATTERNS, REPRODUCTIVE DEVELOPMENT, RESPONSES

2098

Sage, R.F. 1990. A model describing the regulation of ribulose-1,5-bisphosphate carboxylase, electron-transport, and triose phosphate use in response to light-intensity and CO₂ in C3 plants. *Plant Physiology* 94(4):1728-1734.

A model of the regulation of the activity of ribulose-1,5-bis-phosphate carboxylase, electron transport, and the rate of orthophosphate regeneration by starch and sucrose synthesis in response to changes in light intensity and partial pressures of CO₂ and O₂ is presented. The key assumption behind the model is that nonlimiting processes of photosynthesis are regulated to balance the capacity of limiting processes. Thus, at CO₂ partial pressures below ambient, when a limitation on photosynthesis by the capacity of rubisco is postulated, the activities of electron transport and phosphate regeneration are down-regulated in order that the rate of RuBP regeneration matches the rate of RuBP consumption by rubisco. Similarly, at subsaturating light intensity or elevated CO₂, when electron transport or Pi regeneration may limit photosynthesis, the activity of rubisco is downregulated to balance the limitation in the rate of RuBP regeneration. Comparisons with published data demonstrate a general consistency between modelled predictions and measured results.

KEYWORDS: ELEVATED CO₂, GAS-EXCHANGE, INTACT LEAVES, INVIVO, OXYGENASE, PHASEOLUS-VULGARIS L, PHOTOSYNTHESIS, RIBULOSE BISPHOSPHATE CARBOXYLASE, TEMPERATURE, WHEAT SEEDLINGS

2099

Sage, R.F. 1994. Acclimation of photosynthesis to increasing atmospheric CO₂ - the gas-exchange perspective. *Photosynthesis Research* 39(3):351-368.

The nature of photosynthetic acclimation to elevated CO₂ is evaluated from the results of over 40 studies focusing on the effect of long-term CO₂ enrichment on the short-term response of photosynthesis to intercellular CO₂ (the A/C-i response). The effect of CO₂ enrichment on the A/C-i response was dependent on growth conditions, with plants grown in small pots (<5 L) or low nutrients usually exhibiting a reduction of A at a given C-i, while plants grown without nutrient deficiency in large pots or in the field tended to exhibit either little reduction or an enhancement of A at a given C-i following a doubling or tripling of atmospheric CO₂ during growth. Using theoretical interpretations of A/C-i curves to assess acclimation, it was found that when pot size or nutrient deficiency was not a factor, changes in the shape of A/C-i curves which are indicative of a reallocation of resources within the photosynthetic apparatus typically were not observed. Long-term CO₂ enrichment usually had little effect or increased the value of A at all C-i. However, a minority of species grown at elevated CO₂ exhibited gas exchange responses indicative of a reduced amount of

Rubisco and an enhanced capacity to metabolize photosynthetic products. This type of response was considered beneficial because it enhanced both photosynthetic capacity at high CO₂ and reduced resource investment in excessive Rubisco capacity. The ratio of intercellular to ambient CO₂ (the C_i/C_a ratio) was used to evaluate stomatal acclimation. Except under water and humidity stress, C_i/C_a exhibited no consistent change in a variety of C-3 species, indicating no stomatal acclimation. Under drought or humidity stress, C_i/C_a declined in high-CO₂ grown plants, indicating stomata will become more conservative during stress episodes in future high CO₂ environments.

KEYWORDS: C-3 PLANTS, CHENOPODIUM-ALBUM L, ELECTRON-TRANSPORT, ELEVATED CARBON-DIOXIDE, INTACT LEAVES, LONG-TERM EXPOSURE, PHASEOLUS-VULGARIS L, RIBULOSE-1;5- BISPHOSPHATE CARBOXYLASE ACTIVITY, STOMATAL CONDUCTANCE, ULTRAVIOLET-B RADIATION

2100

Sage, R.F. 1995. Was low atmospheric CO₂ during the Pleistocene a limiting factor for the origin of agriculture. *Global Change Biology* 1(2):93-106.

Agriculture originated independently in many distinct regions at approximately the same time in human history. This synchrony in agricultural origins indicates that a global factor may have controlled the timing of the transition from foraging to food-producing economies. The global factor may have been a rise in atmospheric CO₂ from below 200 to near 270 $\mu\text{mol mol}^{-1}$ which occurred between 15,000 and 12,000 years ago. Atmospheric CO₂ directly affects photosynthesis and plant productivity, with the largest proportional responses occurring below the current level of 350 $\mu\text{mol mol}^{-1}$. In the late Pleistocene, CO₂ levels near 200 $\mu\text{mol mol}^{-1}$ may have been too low to support the level of productivity required for successful establishment of agriculture. Recent studies demonstrate that atmospheric CO₂ increase from 200 to 270 $\mu\text{mol mol}^{-1}$ stimulates photosynthesis and biomass productivity of C-3 plants by 25% to 50%, and greatly increases the performance of C-3 plants relative to weedy C-4 competitors. Rising CO₂ also stimulates biological nitrogen fixation and enhances the capacity of plants to obtain limiting resources such as water and mineral nutrients. These results indicate that increases in productivity following the late Pleistocene rise in CO₂ may have been substantial enough to have affected human subsistence patterns in ways that promoted the development of agriculture. Increasing CO₂ may have simply removed a productivity barrier to successful domestication and cultivation of plants. Through effects on ecosystem productivity rising CO₂ may also have been a catalyst for agricultural origins by promoting population growth, sedentism, and novel social relationships that in turn led to domestication and cultivation of preferred plant resources.

KEYWORDS: CLIMATE CHANGE, ELEVATED CARBON-DIOXIDE, GROWTH-RESPONSE, MINERAL NUTRITION, NITROGEN-FIXATION, PHOTOSYNTHETIC ACCLIMATION, PLANTS, RISING CO₂, SOIL ORGANIC MATTER, WATER RELATIONS

2101

Sage, R.F., J. Santrucek, and D.J. Grise. 1995. Temperature effects on the photosynthetic response of C-3 plants to long-term CO₂ enrichment. *Vegetatio* 121(1-2):67-77.

To assess the long-term effect of increased CO₂ and temperature on plants possessing the C-3 photosynthetic pathway, *Chenopodium album* plants were grown at one of three treatment conditions: (1) 23 degrees C mean day temperature and a mean ambient partial pressure of CO₂ equal to 350 μbar ; (2) 34 degrees C and 350 μbar CO₂; and (3) 34 degrees C and 750 μbar CO₂. No effect of the growth treatments was observed on the CO₂ response of photosynthesis, the temperature

response of photosynthesis, the content of Ribulose-1,5-bisphosphate carboxylase (Rubisco), or the activity of whole chain electron transport when measurements were made under identical conditions. This indicated a lack of photosynthetic acclimation in *C. album* to the range of temperature and CO₂ used in the growth treatments. Plants from every treatment exhibited similar interactions between temperature and CO₂ on photosynthetic activity. At low CO₂ (< 300 μbar), an increase in temperature from 25 to 35 degrees C was inhibitory for photosynthesis, while at elevated CO₂ (> 400 μbar), the same increase in temperature enhanced photosynthesis by up to 40%. In turn, the stimulation of photosynthesis by CO₂ enrichment increased as temperature increased. Rubisco capacity was the primary limitation on photosynthetic activity at low CO₂ (195 μbar). As a consequence, the temperature response of A was relatively flat, reflecting a low temperature response of Rubisco at CO₂ levels below its K_m for CO₂. At elevated CO₂ (750 μbar), the temperature response of electron transport appeared to control the temperature dependency of photosynthesis above 18 degrees C. These results indicate that increasing CO₂ and temperature could substantially enhance the carbon gain potential in tropical and subtropical habitats, unless feedbacks at the whole plant or ecosystem level limit the long-term response of photosynthesis to an increase in CO₂ and temperature.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO₂, CHENOPODIUM-ALBUM L, ELEVATED CARBON-DIOXIDE, GAS-EXCHANGE, LIGHT-INTENSITY, NERIUM-OLEANDER, PHASEOLUS-VULGARIS L, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SOURCE-SINK RELATIONS

2102

Sage, R.F., B. Schappi, and C. Korner. 1997. Effect of atmospheric CO₂ enrichment on Rubisco content in herbaceous species from high and low altitude. *Acta Oecologica-International Journal of Ecology* 18(3):183-192.

Atmospheric CO₂ enrichment reduces Rubisco content in many species grown in controlled environments; however, relatively few studies have examined CO₂ effects on Rubisco content of plants grown in their natural habitat. We examined the response of Rubisco content to atmospheric CO₂ enrichment (600-680 $\mu\text{mol mol}^{-1}$ in place of ppm) in 5 herbaceous species growing in a low altitude grassland (550 m) near Basel, Switzerland, and 3 herbaceous species from Swiss alpine grassland at 2470 m. At low elevation, the dominant grass *Bromus erectus* and the subdominant dicot *Sanquisorba miller* exhibited 20% to 25% reduction of Rubisco content following high CO₂ exposure; no CO₂ effect was observed in the subdominants *Carex flacca*, *Lotus corniculatus* and *Trifolium repens*. At the Alpine site, the subdominant grass *Pea alpina* maintained 27% less Rubisco content when grown at high CO₂ while the co-dominant forb *Leontodon helveticus* had 19% less Rubisco in high CO₂: Rubisco content was unaffected in the tundra dominant *Carex curvula*. Because the degree of Rubisco modulation was similar between high and low elevation sites, it does not appear that differences in local partial pressure of CO₂ (altitude) or differences in stress in general induce different patterns of modulation of photosynthetic capacity in response to high CO₂. In addition, the degree of Rubisco reduction (<30%) was less than might be indicated by the low biomass response to CO₂ enrichment previously observed at these sites. Thus, plants in Swiss lowland and alpine grassland appear to maintain greater Rubisco concentration and photosynthetic capacity than whole plants can effectively exploit in terms of harvestable biomass.

KEYWORDS: ALPINE GRASSLAND, C-3, ELEVATED CO₂, EXPRESSION, GROWTH, LEAVES, LIGHT-DEPENDENT REGULATION, PHOTOSYNTHETIC ACCLIMATION, PLANTS

2103

Sage, R.F., T.D. Sharkey, and J.R. Seemann. 1990. Regulation of ribulose-1,5-bisphosphate carboxylase activity in response to light-intensity and CO₂ in the C₃ annuals *Chenopodium album* L and *Phaseolus vulgaris* L. *Plant Physiology* 94(4):1735-1742.

The light and CO₂ response of (a) photosynthesis, (b) the activation state and total catalytic efficiency (K(cata)) of ribulose-1,5-bisphosphate carboxylase (rubisco), and (c) the pool sizes of ribulose 1,5-bisphosphate, (RuBP), ATP, and ADP were studied in the C₃ annuals *Chenopodium album* and *Phaseolus vulgaris* at 25-degrees-C. The initial slope of the photosynthetic CO₂ response curve was dependent on light intensity at reduced light levels only (less than 450 micromoles per square meter per second in C. album and below 200 micromoles per square meter per second in P. vulgaris). Modeled simulations indicated that the initial slope of the CO₂ response of photosynthesis exhibited light dependency when the rate of RuBP regeneration limited photosynthesis, but not when rubisco capacity limited photosynthesis. Measured observations closely matched modeled simulations. The activation state of rubisco was measured at three light intensities in C. album (1750, 550, and 150 micromoles per square meter per second) and at intercellular CO₂ partial pressures (C(i)) between the CO₂ compensation point and 500 microbars. Above a C(i) of 120 microbars, the activation state of rubisco was light dependent. At light intensities of 550 and 1750 micromoles per square meter per second, it was also dependent on C(i), decreasing as the C(i) was elevated above 120 microbars at 550 micromoles per square meter per second and above 300 microbars at 1750 micromoles per square meter per second. The pool size of RuBP was independent of C(i) only under conditions when the activation state of rubisco was dependent on C(i). Otherwise, RuBP pool sizes increases as C(i) was reduced. ATP pools in C. album tended to increase as C(i) was reduced. In P. vulgaris, decreasing C(i) at a subsaturating light intensity of 190 micromoles per square meter per second increased the activation state of rubisco but had little effect on the K(cat). These results support modelled simulations of the rubisco response to light and CO₂, where rubisco is assumed to be down-regulated when photosynthesis is limited by the rate of RuBP regeneration.

KEYWORDS: ABSCISIC- ACID, CHLOROPLAST PROTEIN, GAS-EXCHANGE, INTACT LEAVES, OXYGENASE, PHOTOSYNTHESIS, POOL SIZES, RIBULOSE BISPHOSPHATE CARBOXYLASE, RUBISCO ACTIVASE, WHEAT SEEDLINGS

2104

Sagi, M., A. Dovrat, T. Kipnis, and H. Lips. 1998. Nitrate reductase, phosphoenolpyruvate carboxylase, and glutamine synthetase in annual ryegrass as affected by salinity and nitrogen. *Journal of Plant Nutrition* 21(4):707-723.

The concentration of organic acids, organic nitrogen (N), nitrate (NO₃), and total cations increased in annual ryegrass (*Lolium multiflorum* Lam.) with salinity and N concentration in the growth medium. Increasing salinity and N in the growth medium induced changes in the level of key enzymes of N assimilation and organic acids: nitrate reductase (NR, EC 1.6.6.1), phosphoenolpyruvate carboxylase (PEPc, EC 4.1.1.31), and glutamine synthetase (GS, EC 6.3.1.2). Plants grown in pots filled with sand were irrigated with nutrient solutions with an electroconductivity of 2 or 11.2 dS m(-1) and N applied as ammonium nitrate (NH₄NO₃), sodium nitrate (NaNO₃), or ammonium applied as ammonium nitrate (NH₄NO₃), sodium nitrate (NaNO₃), or ammonium (NH₄) as ammonium sulfate [(NH₄)₂SO₄] at concentrations of 0.5, 4.5 or 9.0 mM. Nitrate reductase, PEPc, and GS increased with salinity and N level. Shoot NR was highest in the presence of NH₄NO₃ irrespective of salinity level, while root NR activity responded best to NO₃. Enhancement of PEPc activity in both shoots and roots was highest with NH₄NO₃ and lowest with NH₄. Nitrogen source had no significant effect on GS activity in shoots or roots of ryegrass. Shoot NR

activity increased with NO₃ concentration in the tissue, as calculated from repression coefficients. The PEPc activity correlated positively with total cations and NO₃ concentrations in the plants, irrespective of the salinity level, suggesting that the increase in total cations and NO₃ induced by salinity may have triggered the changes in enzyme activities. The concentration of organic acids in both shoots and roots correlated positively with PEPc activity irrespective of the salinity level. The PEPc activity was higher in roots than in shoots, while organic acid concentration was higher in shoots. These results suggest that a significant part of the organic acids produced in the roots were used as carbon skeleton for transamination reactions. The increased activity of NR, PEPc, and GS in roots may constitute part of an adaptation strategy of the plant to increasing salinity in the medium. These enzymes have an important role in the metabolism of amino acids and the synthesis of organic N in annual ryegrass irrigated with saline water, and boosting them with suitable N fertilizers could increase the nutritional value and protein content of the crop.

KEYWORDS: ASSIMILATION, CARBON, ENRICHED RHIZOSPHERE CO₂, GROWTH, HIGHER-PLANTS, METABOLISM, NUTRITION, SEEDLINGS, STRESS, TOMATO

2105

Saito, M., T. Homma, Y. Nemoto, and H. Matsuoka. 1993. Intracellular potential change of tradescantia-virginiana L leaf in response to co₂ stress. *Bioelectrochemistry and Bioenergetics* 32(2):133-143.

The response of a Tradescantia virginiana L. leaf to CO₂ stress was measured using a double-barrelled microelectrode (a potential recording electrode and an electrode carrying Lucifer yellow CH dye (LY)). After potential measurement, LY was allowed to diffuse out of the microelectrode by iontophoresis. The position of electrode tip was ascertained from the pattern of LY diffusion. The intracellular potential changed markedly in response to CO₂ stress. The most typical response pattern obtained during CO₂ exposure (ON response) was two-phase, initially changing in the positive direction and then in the negative direction. During the ON response, marked efflux of K⁺ and slight influx of Cl⁻ occurred initially, followed by efflux of Cl⁻ and influx of H⁺. On cessation of CO₂ exposure, the potential showed a similar two-phase pattern (OFF response) but the ion fluxes reversed. Therefore the effect Of CO₂ exposure is not just decrease in intracellular pH owing to dissolution Of CO₂.

KEYWORDS: ELEVATED CO₂, LEAVES, PH MICRO-ELECTRODES, PHOTOSYNTHESIS, PLANT-CELLS

2106

Sala, A., and J.D. Tenhunen. 1996. Simulations of canopy net photosynthesis and transpiration in Quercus ilex L under the influence of seasonal drought. *Agricultural and Forest Meteorology* 78(3-4):203-222.

A mechanistically based C-3 leaf photosynthesis model combined with an empirical stomatal model and a canopy model of light interception and microclimate was used to simulate Quercus ilex canopy net photosynthesis and transpiration at l'Avic watershed (NE Spain). The model takes into account the sun-shade leaf differentiation of photosynthetic characteristics as affected by depth within the canopy. Based on field studies, simulations were carried out for two locations within the watershed along a gradient in elevation, microclimate and forest structure. Effective predictions of diurnal and seasonal courses of stomatal conductance of sun and shade leaves for different days during the year were obtained by changing a single model variable termed g(F). The value of g(F) determined from least squares of observed vs. simulated time courses was linearly related to pre-dawn xylem water

potential over critical ranges of the response curve. Response to $g(F)$ in the model may to a great extent be thought of as the integrated expression of canopy response to root system generated signals or control mechanisms. For development of predictive capability, $g(F)$ is extremely useful because it allows seasonal assessments of water use and carbon dioxide uptake with differing patterns in water availability. Based on simulated responses on representative clear, overcast and variable days throughout the year, only small differences in annual totals for net photosynthesis and transpiration were found between the two sites, despite large differences in soil drying. Annual estimates of canopy water loss were in close agreement with independent estimates of evapotranspiration using the hydrological input/output method.

KEYWORDS: CAPACITY, CARBON GAIN, EFFICIENCY, ELEVATED CO₂, EXCHANGE, FOREST, NITROGEN, OAK, STOMATAL CONDUCTANCE, WATER-USE

2107

Saleska, S.R., J. Harte, and M.S. Torn. 1999. The effect of experimental ecosystem warming on CO₂ fluxes in a montane meadow. *Global Change Biology* 5(2):125-141.

Climatic change is predicted to alter rates of soil respiration and assimilation of carbon by plants. Net loss of carbon from ecosystems would form a positive feedback enhancing anthropogenic global warming. We tested the effect of increased heat input, one of the most certain impacts of global warming, on net ecosystem carbon exchange in a Rocky Mountain montane meadow. Overhead heaters were used to increase the radiative heat flux into plots spanning a moisture and vegetation gradient. We measured net whole-ecosystem CO₂ fluxes using a closed-path chamber system, relatively nondisturbing bases, and a simple model to compensate for both slow chamber leaks and the CO₂ concentration-dependence of photosynthetic uptake, in 1993 and 1994. In 1994, we also measured soil respiration separately. The heating treatment altered the timing and magnitude of net carbon fluxes into the dry zone of the plots in 1993 (reducing uptake by approximate to 100 g carbon m⁻²), but had an undetectable effect on carbon fluxes into the moist zone. During a strong drought year (1994), heating altered the timing, but did not significantly alter the cumulative magnitude, of net carbon uptake in the dry zone. Soil respiration measurements showed that when differences were detected in dry zone carbon fluxes, they were caused by changes in carbon input from photosynthesis, not by temperature-driven changes in carbon output from soil respiration. When differences were detected in dry-zone carbon fluxes, they were caused by changes in carbon input from photosynthesis, not by a temperature-driven changes in carbon output from soil respiration. Regression analysis suggested that the reduction in carbon inputs from plants was due to a combination of two soil moisture effects: a direct physiological response to decreased soil moisture, and a shift in plant community composition from high-productivity species to low-productivity species that are more drought tolerant. These results partially support predictions that warming may cause net carbon losses from some terrestrial ecosystems. They also suggest, however, that changes in soil moisture caused by global warming may be as important in driving ecosystem response as the direct effects of increased soil temperature.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATIC CHANGE, FEEDBACKS, MANIPULATION, PLANT-RESPONSES, SOIL MICROCLIMATE, STORAGE, TEMPERATURE, TRACE GAS FLUXES, VEGETATION

2108

Sallanon, H., B. Dimon, P. Carrier, and P. Chagvardieff. 1995. Effects of CO₂ concentration and irradiance on growth and photosynthesis of *Juglans regia* plantlets grown in-vitro. *Photosynthetica* 31(2):241-249.

Walnut (*Juglans regia* L.) plantlets were incubated during micropropagation in standard vessels (quasi confined vessels) or in aerated vessels flushed with 360 or 20 000 cm³(CO₂) m⁻³ under irradiances of 70 (LI) and 250 (HI) μ mol m⁻² s⁻¹. Plantlet morphology was strongly affected by the environment: leaf surface was increased, but shoot elongation and number of stems were reduced after increasing the irradiance of culture. Gross photosynthesis (P-G) capacity measured by using the O-18(2) isotope and mass-spectrometry techniques was increased by increasing photosynthetic photon flux (PPF) and CO₂ concentration. Plantlets exhibited a potential for photorespiratory activity and Mehler-type reaction and a high rate of mitochondrial respiration in all vessel types and irradiances. When a long-term HI was applied, gas exchange rates (P-G and O-2 uptake) were reduced in most of the vessel and PPF conditions, except in quasi confined vessels. Under all the growth conditions, net photosynthetic rate (P-N) was zero or slightly positive and the dry matter accumulation was very similar. Changes in O-2 exchange, growth rate or enzyme activities linked to carbon fixation that were induced by changes in PFD and CO₂ concentration showed that the photosynthetic characteristics of plantlets were typical for hetero-mixotrophic tissues.

KEYWORDS: ENRICHMENT, FIXATION, INVITRO, LEAVES, LIGHT, O₂, RESPIRATION

2109

Sallanon, H., H. Isaka, B. Dimon, C. Ravel, and P. Chagvardieff. 1997. CO₂ exchanges and nutrient uptake during multiplication and rooting of micropropagated *Juglans regia* plantlets. *Plant Science* 124(1):107-116.

CO₂ gas exchanges in light and dark, PEPC and Rubisco activities and consumption of sugar and mineral nutrients (K⁺, Ca²⁺, Mg²⁺, NH₄⁺, NO₃⁻, PO₄³⁻, SO₄²⁻) were measured during multiplication and rooting stages of in vitro-cultivated *Juglans regia*. CO₂ gas exchanges in light and dark, and PEPC and Rubisco activities varied with plantlet age during a growth cycle. They were higher during the first part of the exponential stage of growth (defined in terms of dry weight increase). Respiratory gas exchanges were always higher than photosynthetic ones. The differences between the two stages of growth were reflected in respiration/photosynthesis and total Rubisco activity/initial Rubisco activity ratios, which were higher in the rooting than in the multiplication stage. This work underlines the need to consider the wide variations in photosynthetic and respiratory gas exchanges related to the plantlet development stage. Mineral absorption also displayed variations, both in the quantity and selectivity of the inorganic nutrients supplied. During the multiplication stage, fast exhaustion of PO₄³⁻ and NH₄⁺ occurred, whereas depletion of Ca²⁺, NH₄⁺, PO₄³⁻ and SO₄²⁻ were observed throughout the rooting stage. The inhibition of photosynthetic activity may be linked to the presence of sugar in the medium and also to ion deficiencies during the multiplication stage. Hence, this work also highlights the importance of mineral elements, suggesting a need to review nutrient medium compositions. (C) 1997 Elsevier Science Ireland Ltd.

KEYWORDS: AERATION, ANATOMY, CULTURE, ENRICHMENT, GROWTH, INVITRO, PHOTOSYNTHESIS

2110

Salt, D.T., G.L. Brooks, and J.B. Whittaker. 1995. Elevated carbon-dioxide affects leaf-miner performance and plant-growth in docks (*Rumex* spp). *Global Change Biology* 1(2):153-156.

Exposure of *R. crispus* and *R. obtusifolius* to elevated CO₂ (600 ppm) resulted in an increased C:N ratio of leaf tissue and greater leaf areas. Larvae of *P. nigritarsis* mining leaves of *X. obtusifolius* during exposure produced significantly bigger mines in elevated than in ambient (350

ppm) conditions. There were no significant treatment effects on pupal weight although in both host species mean weight was greater in ambient than in elevated conditions. These results are consistent with the hypothesis that insect herbivores compensate for increased C:N ratios by increased food consumption. This response by herbivores may partially offset predicted increases in plant biomass in a future high CO₂ environment.

KEYWORDS: CO₂, INSECTS, YIELD

2111

Salt, D.T., P. Fenwick, and J.B. Whittaker. 1996. Interspecific herbivore interactions in a high CO₂ environment: Root and shoot aphids feeding on Cardamine. *Oikos* 77(2):326-330.

This study investigated the effects of elevated CO₂ on populations of root and/or shoot aphids and their effects on partitioning in Cardamine pratensis. Total plant biomass in elevated (approximate to 600 ppm) CO₂ of uninfested Cardamine plants was 52% higher than in ambient (approximate to 350 ppm) concentrations but CO₂ effects were not statistically significant. In elevated CO₂, feeding by shoot aphids (*Aphis fabae fabae*) alone and in combination with root aphids (*Pemphigus populitransversus*), and root aphids alone had no significant effect on plant biomass. No significant effects of elevated CO₂ were detected on population size of the shoot or root-feeding species. Interspecific effects were detected between the root and shoot species. Root aphid populations were significantly smaller in the presence of shoot aphids on the same plants. In this system plant growth was unaffected by an elevated CO₂ environment. Plant species which are more sensitive to elevated CO₂ may show a modified response to herbivore pressure in a future atmospheric environment.

KEYWORDS: COMPETITION, FIELD, GROWTH, HOMOPTERA, INSECT HERBIVORES, PERFORMANCE, PLANT-MEDIATED INTERACTIONS, QUALITY, RESISTANCE, STRESS

2112

Samarakoon, A.B., and R.M. Gifford. 1995. Soil water content under plants at high CO₂ concentration and interactions with the direct CO₂ effects: A species comparison. *Journal of Biogeography* 22(2-3):193-202.

Wheat, maize and cotton, grown as spaced plants in large pots of soil, differed in the way high (2 X ambient) CO₂ concentration affected the time-course of soil water use. For wheat, the tendency to conserve water owing to reduction in stomatal conductance in high CO₂ was largely offset by the stimulation of leaf area development as the soil column dried. However, when the soil was maintained continuously wet, soil water conservation occurred because in the absence of water stress high CO₂ did not maintain a greater leaf area. For maize, which has little or no photosynthetic response to CO₂ concentrations above ambient but a strong stomatal response, water was conserved and the soil profile dried more slowly. Maize leaf area and dry matter growth increased in response to damper soil under high CO₂, despite no growth response to CO₂ in the absence of water stress. For cotton, which has a strong photosynthetic but weak stomatal response to CO₂, the soil column dried faster under high CO₂. Despite this drier soil, cotton still showed the greatest response to high CO₂ of leaf area and dry matter growth of the three species compared. Under wet soil conditions, cotton exhibited a very large leaf area response to CO₂ leading to much greater water use per plant. This contrasts with both wheat and maize which conserved water at high CO₂ when wet. Despite these contrasting transpiration and growth responses, all three species exhibited a relatively similar increase in water use efficiency under high CO₂ for both wet and dry conditions. It is concluded that the secondary effect of high CO₂ on soil water content exerts a strong confounding influence on growth responses to

CO₂. In the longer term, the changed soil water status would influence hydrology, soil microbiology, nutrient relations and species composition. From indirect evidence it is proposed that the relative enhancement of growth owing to CO₂ enrichment is greater under drought conditions than in wet soil because of the effect of water deficit on the intercellular CO₂ concentration in the leaf, C-i. If water deficits cause C-i/C-a to decline then photosynthesis is operating in a more CO₂-sensitive region of the CO₂ response curve.

KEYWORDS: CARBON DIOXIDE, COTTON, FIELD, GROWTH, LEAF, PHOTOSYNTHESIS, STOMATAL CONDUCTANCE, TRANSPIRATION, WHEAT, YIELD

2113

Samarakoon, A.B., and R.M. Gifford. 1996. Elevated CO₂ effects on water use and growth of maize in wet and drying soil (vol 23, pg 53, 1996). *Australian Journal of Plant Physiology* 23(3):401.

2114

Samarakoon, A.B., and R.M. Gifford. 1996. Elevated CO₂ effects on water use and growth of maize in wet and drying soil. *Australian Journal of Plant Physiology* 23(1):53-62.

It is unclear from the literature as to whether growth of C-4 species is responsive to elevated atmospheric CO₂ concentration. Reports vary between no response to strong response. To explore the origin of this discrepancy, spaced plants of maize (*Zea mays*) were grown at atmospheric CO₂ concentrations of 362 or 717 $\mu\text{L L}^{-1}$ under continuously wet or drying soil regimes. The aims were to evaluate the comparative growth promotion from elevated CO₂ in a C-4 plant under the two contrasting water regimes and the causes of any such promotion, and also how water-use efficiency (WUE) is influenced by high CO₂ under the two water regimes. In wet soil, transpiration rate was reduced on average by 29% at high CO₂ but neither total dry matter nor plant height was significantly affected by CO₂ level. Leaf area was not influenced significantly, so daily water use per plant was 25% lower and WUE was increased entirely due to reduced water use at high CO₂. In soil that was drying from field capacity, plants in high CO₂ used about 30% less water than those in ambient CO₂ while the soil was still wet. This resulted in higher soil water content at high CO₂. Plant growth showed a marked response, accumulating 35% more leaf area and 50% more dry matter. Young internodes elongated up to 170% more, giving taller plants. The growth enhancement was largely due to higher average net assimilation rate indicating that C-4 photosynthesis responded to elevated CO₂ during drought. In drying soil the increase in WUE was due to both increased dry matter and reduced water use, the contribution from each depending on the stage of soil drying. We hypothesise therefore that literature examples where maize growth responded to elevated CO₂ may have involved (possibly unrecognised) minor water deficits.

KEYWORDS: AMBIENT, ATMOSPHERIC CO₂, CARBON DIOXIDE, COMMUNITIES, ENRICHMENT, MARSH, PHOTOSYNTHESIS, PLANT GROWTH, RESPONSES, YIELD

2115

Samarakoon, A.B., and R.M. Gifford. 1996. Water use and growth of cotton in response to elevated CO₂ in wet and drying soil (vol 23, pg 63, 1996). *Australian Journal of Plant Physiology* 23(3):401.

2116

Samarakoon, A.B., and R.M. Gifford. 1996. Water use and growth of

cotton in response to elevated CO₂ in wet and drying soil. *Australian Journal of Plant Physiology* 23(1):63-74.

Cotton (*Gossypium hirsutum* cv. Sicala 34) was grown at 352 ('low CO₂') or 710 ('high CO₂') $\mu\text{L L}^{-1}$ atmospheric CO₂ in continuously wet soil, or in drying soil, or in drying soil re-wetted after plant wilting. In wet soil, the approximately 15% reduction in transpiration per unit leaf area owing to high CO₂ was only half that for other species, whereas effects on growth and leaf area were relatively larger. Consequently, water use per plant was 45-50% higher for high CO₂ plants in contrast to other species for which the rate of water use is either the same or lower in high CO₂. Greater plant water use early in a drying cycle caused the soil to dry faster under high CO₂ than under low CO₂. The addition of the consequential greater water stress at high CO₂ in drying soil to the direct CO₂ effect on stomata caused the transpiration rate of high CO₂ plants to fall by up to 60% as the soil dried relative to plants drying at low CO₂. After re-wetting the dry soil, the reduction in transpiration rate at high CO₂ returned within hours to the value of 15% seen in wet soil. The results were inconsistent with the idea that water deficits increase the sensitivity of stomatal aperture to CO₂. Other consequences of drier soil under high CO₂ compared with low CO₂ were: (a) unlike in many other species, in cotton, the relative growth enhancement by high CO₂ is not higher under drying soil compared with wet soil owing to the opposite effect on soil water content; and (b) the increased water-use efficiency in drying soil relative to wet soil was greater in high CO₂ plants than in low CO₂. The confounding of indirect effects of soil water with the direct CO₂ effects may explain the wide variability of literature reports about CO₂ effects on stomatal conductance and water use.

KEYWORDS: ABSCISIC- ACID, ATMOSPHERIC CO₂, CARBON DIOXIDE, FIELD, LEAF, PHOTOSYNTHETIC RATE, PLANT GROWTH, STOMATAL CONDUCTANCE, TRANSPIRATION, YIELD

2117

Samarakoon, A.B., W.J. Muller, and R.M. Gifford. 1995. Transpiration and leaf-area under elevated CO₂ - effects of soil-water status and genotype in wheat. *Australian Journal of Plant Physiology* 22(1):33-44.

Transpiration rate, leaf area expansion, water use and water-use efficiency (WUE) of spaced plants of wheat (cvv. Matong and Quarrior), were examined at ambient and twice ambient CO₂ concentrations in wet and drying soil regimes. A hypothesis tested was that both stomatal conductance (g(s)) and leaf area development are so regulated by the plant in relation to soil water status that the reduction of approximately 40% in g(s) in high CO₂ has no permanent impact on whole-plant water use. Whereas, during a soil drying cycle, leaf area increase under elevated CO₂ counterbalanced closely for reduced g(s) in terms of soil water depletion as reported elsewhere, this counterbalance was neither exact at all times, nor did it apply when the soil was continuously wet. In wet soil, leaf area was not enhanced much by elevated CO₂, probably because, under the high radiation and nutritional conditions used, the tillering rate was almost maximal anyway. Quarrior, having a 40% lower g(s) than Matong genetically, did not counterbalance a reduced transpiration rate with a larger leaf area under either drying or wet soil conditions. These results support rejection, for wheat, of the hypothesis posed; elevated CO₂ increased leaf area mainly by virtue of the direct photosynthetic increase rather than changed soil water status. In wet soil, low g(s) Quarrior had a higher CO₂ effect on WUE (+ 73 to 82%) than did Matong (+ 54 to 65%). In drying soil, both cultivars had a similar increase in WUE at high CO₂ (+ 60 to 68%).

KEYWORDS: AMBIENT, CARBON-DIOXIDE CONCENTRATION, ENRICHMENT, PLANT GROWTH, RESPONSES, RICE, ROOT RESTRICTION, STRESS, TERM, YIELD

2118

Sampson, D.A., E.J. Cooter, P.M. Dougherty, and H.L. Allen. 1996. Comparison of the UKMO and GFDL GCM climate projections in NPP simulations for southern loblolly pine stands. *Climate Research* 7(1):55-69.

We used the process model BIOMASS version 13.0 to simulate contemporary net primary production (NPP) and NPP response to climate projections for a doubling of atmospheric CO₂ concentration from 2 general circulation models (GCMs) that vary in their CO₂ sensitivity: the less sensitive GFDL and the more sensitive UKMO. Increased GCM sensitivity to CO₂ is reflected in increased predictions in the magnitude, variation, and range of the climate variables. Simulations used a 40 yr historical climate record, and 2 stand and site conditions to standardize the total NPP response estimates for eighteen 1x1 degrees grid cells across the southern United States. Contemporary NPP and NPP response estimates from the 18 cells were smoothed using a cell search algorithm to obtain an NPP response index matrix for the entire loblolly pine (*Pinus taeda*) forest-type. We conducted a sensitivity analysis of the environmental variables projected to change in a 2xCO₂ environment to help interpret simulation output. Contemporary NPP varied from 2.5 to 8.5 Mg C ha⁻¹ yr⁻¹ over the range of loblolly pine. High leaf area index (LAI) simulations had 1.5 to 2 times the productivity of low LAI simulations, but the regional patterns were similar; NPP was correlated with regional differences in precipitation and temperature. The NPP response to future climate and atmospheric changes depended on the GCM used, and on the stand and site condition assumed. Inter-annual estimates for the 18 cell simulations resulted in a +22 to +84% NPP response for the GFDL climate projections and a -30 to +94% NPP response for the UKMO climate projections. The 40-year average NPP response for the smoothed data ranged from +43 to +65% and -1 to +94% for the GFDL and the UKMO climate projections, respectively. Consequently, the magnitude and range of the 40-year average NPP response to the climate projections was directly correlated with the GCM CO₂ sensitivity. Although increased CO₂ sensitivity resulted in broader extremes in the predicted temperature response, precipitation response for the 2 models was similar. The NPP response was also correlated with the patterns in predicted climate change, with regional differences coupled to local climatic conditions. Climate projections from both models produced similar NPP responses when predicted temperatures and precipitation regimes were similar. Elevated ambient CO₂ had a greater effect on NPP response than temperature or precipitation in the sensitivity comparisons. Simulations indicate that a CO₂ fertilizer effect, assuming no CO₂ acclimation, more than compensates for declines in productivity over most of the loblolly pine forest-type associated with projected decreased precipitation and/or projected low to moderate increases in temperature and, therefore, increased maintenance respiration costs.

KEYWORDS: CO₂ CONCENTRATIONS, ELEVATED CARBON-DIOXIDE, FORESTS, GROWTH, LEAF-AREA, MODEL, RADIATA, RESPONSES, SLASH PINE, WATER

2119

Sampson, R.N., M. Apps, S. Brown, C.V. Cole, J. Downing, L.S. Heath, D.S. Ojima, T.M. Smith, A.M. Solomon, and J. Wisniewski. 1993. Workshop summary statement - terrestrial biospheric carbon fluxes - quantification of sinks and sources of CO₂. *Water, Air, and Soil Pollution* 70(1-4):3-15.

Understanding the role of terrestrial ecosystems in the global carbon (C) cycle has become increasingly important as policymakers consider options to address the issues associated with global change, particularly climate change. Sound scientific theories are critical in predicting how these systems may respond in the future, both to climate change and human actions. In March 1993, 60 scientists from 13 nations gathered

in Bad Harzburg, Germany, to develop a state-of-the-science assessment of the present and likely future C fluxes associated with the major components of the earth's terrestrial biosphere. In the process, particular emphasis was placed on the potential for improving C sinks and managing long-term C sequestration. The majority of the week's work was conducted in eight working groups which independently considered a particular biome or subject area. The working groups considered: the Global Carbon Cycle; Boreal Forests and Tundra; Temperate Forests; Tropical Forests; Grasslands, Savannas and Deserts; Land and Water Interface Zones; Agroecosystems; and Biomass Management. This paper presents a brief overview of their major conclusions and findings. In addition, Table 1 brings together the best estimates from each group as to the current magnitude and estimated future direction of changes in the terrestrial C fluxes.

2120

Samuelson, L.J., and J.R. Seiler. 1992. Fraser fir seedling gas-exchange and growth in response to elevated CO₂. *Environmental and Experimental Botany* 32(4):351-356.

Growth and gas exchange characteristics were examined in Fraser fir (*Abies fraseri* (Pursh.) Poir.) seedlings grown from seed in elevated (713 ppm) or ambient (374 ppm) CO₂ for 1 year (two artificial growing seasons) to determine the potential influence of a twice-ambient CO₂ concentration on this species. A subset of seedlings was transplanted from 172 cm³ pots into 1000 cm³ pots at 7 months to determine if CO₂ effects were dependent on rooting volume. At 5 and 12 months, net photosynthesis (P_{net}) and leaf conductance (g_l) were lower in elevated CO₂-grown seedlings grown in 172 cm³ pots than in ambient CO₂-grown seedlings when measured at either 346 or 796 ppm CO₂. For 12-month-old seedlings grown in 1000 cm³ pots, P_{net} was reduced by an elevated CO₂ growth environment only when measured at 346 ppm CO₂, although g_l was lower in these seedlings when measured at either CO₂ measurement level. Seedlings grown in both pot sizes and in elevated CO₂ for 1 year had greater height, diameter, and leaf, stem, root and total dry weights than seedlings grown in ambient CO₂. Specific leaf weight (SLW) was greater in elevated than in ambient CO₂-grown needles only in the large pot size treatment. These results suggest that Fraser fir seedling growth will increase in a future elevated CO₂ environment despite changes in gas exchange characteristics.

KEYWORDS: ATMOSPHERIC CO₂, INCREASE

2121

Samuelson, L.J., and J.R. Seiler. 1993. Interactive role of elevated CO₂, nutrient limitations, and water-stress in the growth-responses of red spruce seedlings. *Forest Science* 39(2):348-358.

Red spruce (*Picea rubens* Sarg.) seedlings were grown from seed for 5 mo in ambient (362 ppm) or elevated (711 ppm) CO₂ to determine the potential effect of an increase in global CO₂ concentration on seedling growth and establishment. CO₂ exposure treatments were crossed with two levels of soil fertility and water stress treatments to determine if seedling dry weight, size, and fixed growth responses to elevated CO₂ depended on nutrient and water supply. Seedling dry weight and size responses to elevated CO₂ at 5 mo did not depend on nutrient and water supply. Seedlings grown in both soil fertility treatments and water stress treatments responded similarly to CO₂ treatment. Water stress and CO₂ treatments did have an interactive influence on the fixed growth potential of the terminal leader. Leaf weight, leaf area, and height of the terminal leader of water-stressed seedlings were greater in seedlings exposed to elevated CO₂ during budset than seedlings exposed to ambient CO₂. Total new fixed growth (lateral plus terminal) and total terminal fixed growth (leaf plus stem) were greater in seedlings that formed shoot primordia in elevated CO₂ than in ambient CO₂. Red

spruce seedlings grown in elevated CO₂ for 5 mo had greater stem diameter, height, branching density, leaf weight, root weight, stem weight, total weight, and mean relative growth rate (RGR) from 3 to 5 mo than seedlings grown in ambient CO₂. Red spruce seedling responses to elevated CO₂ suggest that seedling establishment in natural environments may be enhanced when ambient CO₂ concentrations rise even if water and nutrient availabilities are limited.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, NUTRITION, PATTERNS, PINE, STANDS

2122

Samuelson, L.J., and J.R. Seiler. 1994. Red spruce seedling gas-exchange in response to elevated CO₂, water-stress, and soil fertility treatments. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 24(5):954-959.

The interactive influences of ambient (374 µL.L⁻¹) or elevated (713 µL.L⁻¹) CO₂, low or high soil fertility, well-watered or water-stressed treatment, and rooting volume on gas exchange and growth were examined in red spruce (*Picea rubens* Sarg.) grown from seed through two growing seasons. Leaf gas exchange throughout two growing seasons and growth after two growing seasons in response to elevated CO₂ were independent of soil fertility and water-stress treatments, and rooting volume. During the first growing season, no reduction in leaf photosynthesis of seedlings grown in elevated CO₂ compared with seedlings grown in ambient CO₂ was observed when measured at the same CO₂ concentration. During the second growing season, net photosynthesis was up to 21% lower for elevated CO₂-grown seedlings than for ambient CO₂-grown seedlings when measured at 358 µL.L⁻¹. Thus, photosynthetic acclimation to growth in elevated CO₂ occurred gradually and was not a function of root-sink strength or soil-fertility treatment. However, net photosynthesis of seedlings grown and measured at an elevated CO₂ concentration was still over 2 times greater than the photosynthesis of seedlings grown and measured at an ambient CO₂ concentration. Growth enhancement by CO₂ was maintained, since seedlings grown in elevated CO₂ were 40% larger in both size and weight after two growing seasons.

KEYWORDS: CARBON DIOXIDE, ENRICHMENT, GROWTH-RESPONSES, NUTRIENT-UP TAKE, PHOTOSYNTHESIS, PHYSIOLOGY, RISING CO₂, STANDS, TREES

2123

Sanders, I.R., R. Streitwolf-Engel, M.G.A. van der Heijden, T. Boller, and A. Wiemken. 1998. Increased allocation to external hyphae of arbuscular mycorrhizal fungi under CO₂ enrichment. *Oecologia* 117(4):496-503.

Prunella vulgaris was inoculated with different arbuscular mycorrhizal fungi (AMF) and grown at two concentrations of CO₂ (ambient, 350 µL.L⁻¹, and elevated, 600 µL.L⁻¹) to test whether a plant's response to elevated CO₂ is dependent on the species of AMF colonizing the roots. Using compartments accessible only to AMF hyphae but not to roots, we also tested whether elevated CO₂ affects the growth of external AMF hyphae. Plant biomass was significantly greater at elevated than at ambient CO₂; the biomass of the root system, for example, increased by a factor of 2. The colonization of AMF inside the root remained constant, indicating that the total AMF inside the root system also increased by a factor of 2. The length of external AMF hyphae at elevated CO₂ was up to 5 times that at ambient CO₂, indicating that elevated CO₂ promoted allocation of AMF biomass to the external hyphae. The concentration and content of phosphorus in the stolons differed significantly between ambient and elevated CO₂ but this resulted in either an increase or a decrease, according to which AMF isolate occupied the roots. We hypothesized that an increase in external

hyphal growth at elevated CO₂ would result in increased P acquisition by the plant. To test this we supplied phosphorus, in a compartment only accessible to AMF hyphae. Plants did not acquire more phosphorus at elevated CO₂ when phosphorus was added to this compartment. Large increases in AMF hyphal growth could, however, play a significant role in the movement of fixed carbon to the soil and increase soil aggregation.

KEYWORDS: CARBON DIOXIDE, COLONIZATION, ELEVATED CO₂, GROWTH, ROOTS

2124

Santrucek, J., and R.F. Sage. 1996. Acclimation of stomatal conductance to a CO₂-enriched atmosphere and elevated temperature in *Chenopodium album*. *Australian Journal of Plant Physiology* 23(4):467-478.

Acclimation of stomatal conductance to different CO₂ and temperature regimes was determined in *Chenopodium album* L. plants grown at one of three treatment conditions: 23 degrees C and 350 μ mol CO₂ mol⁻¹ air; 34 degrees C and 350 μ mol mol⁻¹; and 34 degrees C and 750 μ mol mol⁻¹. Stomatal conductance (g(s)) as a function of intercellular CO₂ (C_i) was determined for each treatment at 25 and 35 degrees C, and these data were used to estimate gains of the feedback loops linking changes in intercellular CO₂ with stomatal conductance and net CO₂ assimilation. Growth temperature affected the sensitivity of stomata to measurement temperature in a pattern that was influenced by intercellular CO₂. Stomatal conductance more than doubled at intercellular CO₂ varying between 200 and 600 μ mol mol⁻¹ as leaf temperature increased from 25 to 35 degrees C for plants grown at 23 degrees C. In contrast, stomatal conductance was almost unaffected by measurement temperature in plants grown at 34 degrees C. Elevated growth CO₂ attenuated the response of stomatal conductance to CO₂, but growth temperature did not. Stomatal sensitivity to C_i was extended to higher C_i in plants grown in elevated CO₂. As a result, plants grown at 750 μ mol mol⁻¹ CO₂ had higher C_i/C_a at ambient CO₂ values between 300 and 1200 μ mol mol⁻¹ than plants grown at 350 μ mol mol⁻¹ CO₂. The gain of the stomatal loop was reduced in plants grown at elevated CO₂ or at lower temperature when compared to plants grown at 350 μ mol mol⁻¹ and 34 degrees C. Both photosynthetic and stomatal loop gains acclimated to elevated CO₂ in proportion so that their ratio, integrated over the range of C_i in which the plant operates, remained constant. Water use efficiency (WUE) more than doubled after a short-term doubling of ambient CO₂. However, the WUE of plant grown and measured at elevated CO₂ was only about 1.5 times that of plant transiently exposed to elevated CO₂, due to stomatal acclimation. An optimal strategy of water use was maintained for all growth treatments.

KEYWORDS: C-3 PLANTS, CARBONDIOXIDE, CO₂ ASSIMILATION, GAIN, HUMIDITY, LEAF CONDUCTANCE, LIGHT, PHOTOSYNTHESIS, RESPONSES, WATER-USE EFFICIENCY

2125

Santrucek, J., H. Santruckova, J. Kveton, M. Simkova, and K. Rohacek. 1994. The effect of elevated CO₂ concentration on photosynthetic CO₂ fixation, respiration and carbon economy of wheat plants. *Rostlinna Vyroba* 40(8):689-696.

Winter wheat plants were grown under controlled atmospheric and light conditions for 25 days to assess the response of photosynthesis, respiration and carbon allocation to elevated ambient CO₂ concentration. Daily balance of carbon fixation and loss was measured separately for shoots and roots including root exudation. Doubled CO₂ (700 μ mol CO₂ mol⁻¹) stimulated photosynthetic CO₂ uptake and dark respiration rate when calculated on the leaf area basis. However,

total daily carbon gain per plant and total dry matter of shoot was lower for high-CO₂-grown plants due to reduced leaf area. After 23 days of exposition to high CO₂, photosynthesis was depressed probably due to limiting regeneration of ribulose biphosphate. Both stomatal resistance and water use efficiency were markedly higher in high-CO₂-grown plants. Higher evaporative demand in low-CO₂-grown plants promoted root elongation. Total root length was 160% of that in high-CO₂-grown plants. Root exudation of high-CO₂-grown plants was higher in the first days of plant development, but the inhibition of net photosynthesis was followed by a decrease in exudation.

2126

Santruckova, H., J. Santrucek, J. Kveton, M. Simkova, D. Elhottova, and K. Rohacek. 1999. Carbon balance of a winter wheat-root microbiota system under elevated CO₂. *Photosynthetica* 36(3):341-354.

We examined the carbon budget of young winter wheat plants and their associated microorganisms as affected by a doubling of the atmospheric CO₂ concentration (700 μ mol mol⁻¹). Plants were grown hydroponically in pre-sterilised sand at a controlled irradiance and temperature regime. Net photosynthesis (P-N) and respiration (R-D) rates of roots and shoots were measured continuously, plant growth and carbon distribution in the plant-root medium-associated microorganism system were determined destructively in interval-based analyses. P-N in elevated CO₂ grown plants (EC) was 123 % of that in the control (AC) plants when averaged over the whole life span (39-d-old plants, 34 d in EC), but the percentage varied with the developmental stage being 115, 88, and 167 % in the pretiltering, tillering, and posttiltering phase, respectively. There was a transient depression of P-N, higher amplitude of day/night fluctuations of the chloroplast starch content, and depression of carbon content in rhizosphere of EC plants during the period of tillering. After 34 d in EC, carbon content in shoots, roots, and in rhizodepositions was enhanced by the factors 1.05, 1.28, and 1.96, respectively. Carbon partitioning between above and belowground biomass was not affected by EC, however, proportionally more C in the belowground partitioning was allocated into the root biomass. Carbon flow from roots to rhizodepositions and rhizosphere microflora was proportional to P-N; its fraction in daily assimilated carbon decreased from young (17 %) to older (3-4 %) plants.

KEYWORDS: ATMOSPHERIC CO₂, ENRICHMENT, GAS-EXCHANGE, GROWTH, NITROGEN, PHOTOSYNTHESIS, RESPONSES, RHIZOSPHERE, SOIL, TRITICUM-AESTIVUM L

2127

Santruckova, H., and M. Simek. 1997. Effect of soil CO₂ concentration on microbial biomass. *Biology and Fertility of Soils* 25(3):269-273.

The effect of increasing soil CO₂ concentration was studied in six different soils. The soils were incubated in ambient air (0.05 vol.% CO₂) or in air enriched with CO₂ (up to 5.0 vol.% CO₂). Carbon dioxide evolution, microbial biomass, growth or death rate quotients and glucose decay rate were measured at 6, 12 and 24 h of CO₂ exposure. The decrease in soil respiration ranged from 7% to 78% and was followed by a decrease in microbial biomass by 10-60% in most cases. High CO₂ treatments did not affect glucose decay rate but the portion of C-gluc mineralized to CO₂ was lowered and a larger portion of C-gluc remained in soils. This carbon was not utilized by soil microorganisms.

KEYWORDS: CARBON DIOXIDE, LAND, MICROORGANISMS, RESPIRATION

2128

Saralabai, V.C., M. Vivekanandan, and R.S. Babu. 1997. Plant responses to high CO₂ concentration in the atmosphere. *Photosynthetica* 33(1):7-37.

The impact of continuous rise in ambient CO₂ concentration (AC) in the atmosphere on different facets of growth of crop plants is assessed. The effects of CO₂ enrichment (EC) on plant growth, C-3 and C-4 photosynthesis, source-sink ratio, partitioning and translocation of metabolites, photosynthetic enzymes, respiratory rate, leaf area index, stomatal conductance (g(s)), transpiration rate, biomass production and water use efficiency are reviewed. The CO₂ fertilization effects are studied in both short-term (open top chambers) and long-term experiments. Long-term experiments suggest that ribulose-1,5-bisphosphate carboxylase is inactivated at high CO₂ concentrations. Also g(s) is lowered. One of the conspicuous effects of EC is the closure of stomata in C-3 plants. Photosystem (PS) 2 electron transport is more affected than PS1. Starch is the immediate product accumulated in the leaf of C-3 plants. The "CO₂ fertilization effect" does not confer any great advantage even in C-3 plants.

KEYWORDS: DARK RESPIRATION, DRY-MATTER PRODUCTION, ELEVATED CARBON-DIOXIDE, LOLIUM-PERENNE, LONG-TERM EXPOSURE, PHASEOLUS-VULGARIS, RIBULOSE-1:5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SOYBEAN CANOPY PHOTOSYNTHESIS, SWEET-POTATO, WATER-USE EFFICIENCY

2129

Sasek, T.W., and B.R. Strain. 1990. Implications of atmospheric CO₂ enrichment and climatic-change for the geographical-distribution of 2 introduced vines in the USA. *Climatic Change* 16(1):31-51.

2130

Sasek, T.W., and B.R. Strain. 1991. Effects of CO₂ enrichment on the growth and morphology of a native and an introduced honeysuckle vine. *American Journal of Botany* 78(1):69-75.

Japanese honeysuckle (*Lonicera japonica* Thunb.), introduced to the United States, and the native coral honeysuckle (*Lonicera sempervirens* L.) were compared to determine how intrinsic differences in their growth characteristics would affect their response to atmospheric carbon dioxide enrichment. Plants of both species grown from cuttings were harvested after 54 days of growth in controlled environment growth chambers at 350, 675, or 1,000- μ l/liter CO₂. The biomass of Japanese honeysuckle was increased 135% at 675- μ l/liter CO₂ and 76% at 1,000- μ l/liter CO₂ after 54 days. Morphologically, the main effect of CO₂ enrichment was to triple the number of branches and to increase total branch length six times. Enhanced and accelerated branching also increased total leaf area 50% at elevated CO₂ concentrations. In coral honeysuckle, total biomass was only 40% greater in the elevated CO₂ treatments. Branching was quadrupled but had not proceeded long enough to affect total leaf area. Main stem height was increased 36% at 1,000- μ l/liter CO₂. The much less significant height response of other woody erect growth forms suggests that vines may increase in importance during competition if atmospheric CO₂ concentrations increase as predicted. The impact of Japanese honeysuckle in the United States may become more serious.

KEYWORDS: ATMOSPHERIC CO₂, CARBON-DIOXIDE ENRICHMENT, CLIMATE, KUDZU PUERARIA-LOBATA, LIQUIDAMBAR-STYRACIFLUA

2131

Sato, H., N. Sakurai, S. Sendo, H. Saneoka, H. Nobuyasu, and K. Fujita. 1997. Factors affecting leaf area development in husk leaf of

flint corn. *Crop Science* 37(6):1826-1831.

Some corn (*Zea mays* L.) genotypes produce husk leaves (laminae extending from the husk) that on a per unit area basis, contribute more photosynthate to grain production than culm leaves. Furthermore, a high correlation between husk leaf area and dry weight has been observed, but little is known about the changes in cell components during development of husk leaves. A field experiment was conducted to quantify methanol (MeOH)-soluble fraction (cytosol) and incorporation of C-13-labeled photosynthate in cell walls from 9 d before silking (DBS) to silking. The ear leaf of flint corn (F-1 of N-19 by X-15) was subjected to (CO₂)-C-13, eight DBS. Leaf area, dry weight, and photosynthetic activity of the husk leaves, and sugar content of various cell components were measured continuously during the 9-d period. The husk leaf attained one-half of its maximum apparent photosynthetic rate (P-0.) when it had 8% of its maximum leaf area at 4 DES. At 9 DBS, neutral sugars in the MeOH-soluble fraction accounted for most of nonstarch carbohydrates within the husk leaf (68%), while hemicellulose and cellulose fractions accounted for <10%. At silking, however, sugars in the hemicellulose and cellulose fractions increased by 23 and 56%, respectively. Results of (CO₂)-C-13 labeling suggest that during rapid husk leaf development, MeOH-soluble fraction decreases, while the hemicellulose fraction fluctuates, and cellulose fraction increases.

KEYWORDS: DRY-MATTER, ELEVATED CO₂, EXTENSION, GROWTH, HYPOCOTYLS, LEAVES, SWEET CORN, WALLS

2132

Saurer, M., S. Maurer, R. Matyssek, W. Landolt, M.S. Gunthardtgoerg, and U. Siegenthaler. 1995. The influence of ozone and nutrition on delta-C-13 in betula-pendula. *Oecologia* 103(4):397-406.

In the cellulose of stems and leaves, delta(13)C was investigated in a birch clone (*Betula pendula*), which was exposed throughout the growing season to either <3 (control) or 90/40 nl O-3 1(-1) (day/night). Each regime was split into plants under high or low nutrient supply. delta(13)C was increased (becoming less negative), in stems rather than leaves, by both high nutrition (+2 parts per thousand) and O-3 stress (+1 parts per thousand). Whereas high nutrition raised the water-use efficiency (WUE) while lowering the CO₂ concentration in the inner leaf air space (c(i)), WUE decreased and c(i) increased under O-3 stress. Therefore, only the nutritional effect on the carbon isotope fractionation was reproduced by the model of Farquhar et al. (1982) which estimates WUE by means of delta(13)C based on C-i, C-i was not biased by 'patchiness' in respect to stomatal opening. The latter was verified by microscopical analysis and the complete water infiltration of the birch leaves through the stomata, independent of the diurnal course of the leaf conductance for water vapour. Under low nutrient supply, the activity of phosphoenol pyruvate carboxylase (PEPC) was roughly doubled by ozone to about 1.3% of the total carboxylation capacity (by PEPC + rubisco), and was increased to 1.7% under high nutrition. The fractionation model, extended to account for varying activities of the carboxylating enzymes, indicated that stimulated PEPC was the cause of elevated delta(13)C, although c(i) was increased under O-3 stress. The stimulation of PEPC and, as a consequence, elevated delta(13)C are discussed as part of a whole-plant acclimation to O-3 stress.

KEYWORDS: ABSCISIC-ACID, BIRCH LEAVES, CARBON ISOTOPE DISCRIMINATION, CO₂, DECLINE, GAS-EXCHANGE, GROWTH, NET PHOTOSYNTHESIS, PLANTS, WATER-VAPOR EXCHANGE

2133

Saxe, H. 1994. Relative sensitivity of greenhouse pot plants to long-term exposures of no-containing and no2-containing air. *Environmental Pollution* 85(3):283-290.

Thirty-five cultivars of pot plants of 20 families were exposed for 50-64 days in a greenhouse facility to either 1 mul litre-1 NO with 0.5 mul litre-1 NO₂, or 1 mul litre-1 NO₂ with 0.1 mul litre-1 NO for 15 h each day, with air which was free from these gases as the reference. A sensitivity ranking of the pot plants was compiled, with the highest priority on visible injuries, followed by growth reductions, primarily as a response to the NO-dominated exposures, simulating the NO(x)-polluted environment in direct-fired, CO₂-enriched greenhouses. This treatment reduced the leaf dry weight more than the number and area of the leaves. Twenty-two cultivars were significantly injured, while two (*Hibiscus* sp., *Epipremnum pinnatum*, green) were significantly improved. The NO(x)-sensitivity of pot plants was highest in cultivars with variegated, small or narrow leaves, and in the Moraceae family. Nine cultivars (*Ficus elastica* 'Robusta', *F. benjamina*, *F. pumila* 'Sonny', *Dieffenbachia maculata* 'Camilla', *F. elastica* 'Tineke', *Epipremnum pinnatum* 'Marble Queen', *Begonia elatior* 'Nelson', *Cyclamen persica*, *Poinsettia* 'Mini') were specifically sensitive to the NO-containing exposure; six were specifically sensitive to the NO₂-containing exposure (*F. elastica* 'Robusta', *Asparagus* den. 'Sprenger', *Hedera helix* 'Shamrock', *Aspidium nidus*, *Aster novo-belgii*, *Hypoestes* phyl. 'Betina'); and 12 (*Soleirolia soleirolia*, *Asparagus* den. 'Sprenger', *H. helix* 'Ester', *Codiaeum Pictum*, *Rosa* 'Minimo Red', *F. benjamina* 'Starlight', *Saintpaulia ionantha* 'light blue', *F. pumila*, *Rhododendron simsii*, *H. helix* 'Shamrock', *Hibiscus* sp., *E. pinnatum*) were equally sensitive to mixtures dominated by either gas, as measured by at least one response parameter.

KEYWORDS: CARBON DIOXIDE, CO₂, NET PHOTOSYNTHESIS, NITROGEN-DIOXIDE, OXIDES, POLLUTION

2134

Saxe, H., D.S. Ellsworth, and J. Heath. 1998. Tree and forest functioning in an enriched CO₂ atmosphere. *New Phytologist* 139(3):395-436.

Forests exchange large amounts of CO₂ with the atmosphere and can influence and be influenced by atmospheric CO₂. There has been a recent proliferation of literature on the effects of atmospheric CO₂ on forest trees. More than 300 studies of trees on five different continents have been published in the last five years. These include an increasing number of field studies with a long-term focus and involving CO₂ x stress or environment interactions. The recent data on long-term effects of elevated atmospheric CO₂ on trees indicate a potential for a persistent enhancement of tree growth for several years, although the only relevant long-term datasets currently available are for juvenile trees. The current literature indicates a significantly larger average long-term biomass increment under elevated CO₂ for conifers (130%) than for deciduous trees (49%) in studies not involving stress components. However, stimulation of photosynthesis by elevated CO₂ in long-term studies was similar for conifers (62 %) and deciduous trees (53 %). Recent studies indicate that elevated CO₂ causes a more persistent stimulation of biomass increment and photosynthesis than previously expected. Results of seedling studies, however, might not be applicable to other stages of tree development because of complications of age- dependent and size-dependent shifts in physiology and carbon allocation, which are accelerated by elevated CO₂. In addition, there are many possible avenues to down-regulation, making the predicted canopy CO₂ exchange and growth of mature trees and forests in a CO₂-rich atmosphere uncertain. Although, physiological down-regulation of photosynthetic rates has been documented in field situations, it is rarely large enough to offset entirely photosynthetic gains in elevated CO₂. A persistent growth stimulation of individual mature trees has been demonstrated although this effect is more uncertain in trees in natural stands. Resource interactions can both constrain tree responses to elevated CO₂ and be altered by them. Although drought can reduce gas-exchange rates and offset the benefits of elevated CO₂, even in well watered trees, stomatal conductance is remarkably less responsive to

elevated CO₂ than in herbaceous species. Stomata of a number of tree species have been demonstrated to be unresponsive to elevated CO₂. We conclude that positive effects of CO₂ on leaf area can be at least as important in determining canopy transpiration as negative, direct effects of CO₂ on stomatal aperture. With respect to nutrition, elevated CO₂ has the potential to alter tree-soil interactions that might influence future changes in ecosystem productivity. There is continued evidence that in most cases nutrient limitations diminish growth and photosynthetic responses to elevated CO₂ at least to some degree, and that elevated CO₂ can accelerate the appearance of nutrient limitations with increasing time of treatment. In many studies, tree biomass responses to CO₂ are artefacts in the sense that they are merely responses to CO₂-induced changes in internal nutritional status of the tree. There are numerous interactions between CO₂ and factors of the biotic and abiotic environment. The importance of increasing atmospheric CO₂ concentrations for productivity is likely to be overestimated if these are not taken into account. Many interactions, however, are simply additive rather than synergistic or antagonistic. This appears to hold true for many parameters under elevated CO₂ in combination with temperature, elevated O₃, and other atmospheric pollutants. However, there is currently little evidence that elevated CO₂ will counteract O₃ damage. When the foliage content of C, mineral nutrients and secondary metabolites is altered by elevated CO₂, tree x insect interactions are modified. In most trees, mycorrhizal interactions might be less important for direct effects of CO₂ than for alleviating general nutrient deficiencies. Since many responses to elevated CO₂ and their interactions with stress show considerable variability among species/genotypes, one principal research need is for comparative studies of a large variety of woody species and ecosystems under realistic conditions. We still need more long-term experiments on mature trees and stands to address critical scaling issues likely to advance our understanding of responses to elevated CO₂ at different stages of forest development and their interactions with climate and environment. The only tools available at present for coping with the consequences of rising CO₂ are management of resources and selection of genotypes suitable for the future climate and environment.

KEYWORDS: BEECH FAGUS- SYLVATICA, BETULA-PENDULA ROTH, CO₂-INDUCED GROWTH ENHANCEMENTS, ELEVATED CARBON-DIOXIDE, GAS-EXCHANGE RESPONSES, LONG-TERM EXPOSURE, PICEA-ABIES L, PONDEROSA PINE- SEEDLINGS, SITCHENSIS BONG CARR, WATER-LOSS REGULATION

2135

ScarasciaMugnozza, G., P. DeAngelis, G. Matteucci, and R. Valentini. 1996. Long-term exposure to elevated [CO₂] in a natural *Quercus ilex* L community: Net photosynthesis and photochemical efficiency of PSII at different levels of water stress. *Plant, Cell and Environment* 19(6):643-654.

Naturally grown trees of Mediterranean evergreen oak (*Quercus ilex* L.), representing the climax species of the region, were enclosed in six large open-top chambers and exposed to ambient and elevated CO₂ concentrations during a 3 year period. Maximum daily net photosynthetic rates measured at the two different CO₂ concentrations were from 30 to 100% higher in elevated than in ambient [CO₂] throughout the experimental period. The increase in maximum daily photosynthesis was also accompanied by a 93% rise in the apparent quantum yield of CO₂ assimilation, measured during periods of optimum soil moisture conditions. Hence, no clear evidence of downregulation of net photosynthetic activity was found. Interactions between atmospheric CO₂ concentration and plant water stress were studied by following the natural evolution of drought in different seasons and years. At each level of water stress, the maximum rate of carbon assimilation was higher in elevated than in ambient [CO₂] by up to 100%. Analysis of in vivo chlorophyll fluorescence parameters in normal (21%) and low (2%) oxygen concentrations provided useful insights into

the functioning and stability of the photosynthetic processes, The photochemical efficiency of PSII (F-v/F-m) progressively decreased as drought conditions became more evident; this trend was accentuated under elevated [CO₂]. Thermal de-excitation processes were possibly more significant under elevated than under ambient [CO₂], in a combination of environmental stresses. This research suggests two possible conclusions: (i) a 'positive' interaction between elevated [CO₂] and carbon metabolism can be obtained through relief of water stress limitation in the summer months, and (ii) elevated [CO₂], under drought conditions, may also enhance the significance of slow- relaxing quenching.

KEYWORDS: CARBON DIOXIDE, CHLOROPHYLL FLUORESCENCE, ELECTRON-TRANSPORT, GAS-EXCHANGE, LEAVES, O-2 EVOLUTION, PHOTON YIELD, PHOTOSYSTEM, QUANTUM YIELDS, VASCULAR PLANTS

2136

Schaffer, B., C. Searle, A.W. Whiley, and R.J. Nissen. 1996. Effects of atmospheric CO₂ enrichment and root restriction on leaf gas exchange and growth of banana (Musa). *Physiologia Plantarum* 97(4):685-693.

The effects of atmospheric CO₂ enrichment and root restriction on photosynthetic characteristics and growth of banana (Musa sp, AAA cv. Gros Michel) plants were investigated. Plants were grown aeroponically in root chambers in controlled environment glasshouse rooms at CO₂ concentrations of 350 or 1000 $\mu\text{mol CO}_2 \text{ mol}^{-1}$. At each CO₂ concentration, plants were grown in large (200 l) root chambers that did not restrict root growth or in small (20 l) root chambers that restricted root growth. Plants grown at 350 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ generally had a higher carboxylation efficiency than plants grown at 1000 $\mu\text{mol CO}_2 \text{ mol}^{-1}$, although actual net CO₂ assimilation (A) was higher at the higher ambient CO₂ concentration due to increased intercellular CO₂ concentrations (C_i) resulting from CO₂ enrichment. Thus, plants grown at 1000 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ accumulated more leaf area and dry weight than plants grown at 350 $\mu\text{mol CO}_2 \text{ mol}^{-1}$. Plants grown in the large root chambers were more photosynthetically efficient than plants grown in the small root chambers. At 350 $\mu\text{mol CO}_2 \text{ mol}^{-1}$, leaf area and dry weights of plant organs were generally greater for plants in the large root chambers compared to those in the small root chambers. Atmospheric CO₂ enrichment may have compensated for the effects of root restriction on plant growth since at 1000 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ there was generally no effect of root chamber size on plant dry weight.

KEYWORDS: AAA, CAVENDISH SUBGROUP, ELEVATED CARBON-DIOXIDE, LEAVES, LIGHT, PHOTOSYNTHETIC ACCLIMATION, PHYSIOLOGICAL-RESPONSES, PLANTS, STRESS, SUBTROPICS

2137

Schaffer, B., A.W. Whiley, and C. Searle. 1999. Atmospheric CO₂ enrichment, root restriction, photosynthesis, and dry-matter partitioning in subtropical and tropical fruit crops. *Hortscience* 34(6):1033-1037.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, ELEVATED CO₂, GENE-EXPRESSION, GROWTH, LEAF GAS- EXCHANGE, LEAVES, NET PHOTOSYNTHESIS, NITROGEN, PLANTS, SOUR ORANGE TREES

2138

Schaffer, B., A.W. Whiley, C. Searle, and R.J. Nissen. 1997. Leaf gas exchange, dry matter partitioning, and mineral element concentrations in mango as influenced by elevated atmospheric carbon dioxide and root restriction. *Journal of the American Society for Horticultural Science*

122(6):849-855.

The effects of atmospheric CO₂ enrichment and root restriction on net CO₂ assimilation (A), dry mass partitioning, and leaf mineral element concentrations in 'Kensington' and 'Tommy Atkins' mango (*Mangifera indica* L.) were investigated. Trees were grown in controlled-environment glasshouse rooms at ambient CO₂ concentrations of 350 or 700 $\mu\text{mol mol}^{-1}$. At each CO₂ concentration, trees were grown in 8-L containers, which restricted root growth, or grown aeroponically in 200-L root mist chambers, which did not restrict root growth. Trees grown in 350 $\mu\text{mol mol}^{-1}$ CO₂ were more efficient at assimilating CO₂ than trees grown in 700 $\mu\text{mol mol}^{-1}$ CO₂. However, total plant and organ dry mass was generally higher for plants grown at 700 $\mu\text{mol mol}^{-1}$ CO₂ due to increased A as a result of a greater internal partial pressure of CO₂ (C_i) in leaves of plants in the CO₂ enriched environment. Root restriction reduced A resulting in decreased organ and plant dry mass. In root-restricted plants, reduced A and dry matter accumulation offset the increases in these variables resulting from atmospheric CO₂ enrichment. Atmospheric CO₂ enrichment and root restriction did not affect dry mass partitioning. Leaf mineral element concentrations were generally lower for trees grown at the higher ambient CO₂ concentration, presumably due to a dilution effect from an increased growth rate.

KEYWORDS: CO₂- ENRICHMENT, GROWTH, NITROGEN, PHOTOSYNTHETIC ACCLIMATION, PLANTS, RESPONSES, WHEAT

2139

Schapendonk, A.H.C.M., P. Dijkstra, J. Groenwold, C.S. Pot, and S.C. vandeGeijn. 1997. Carbon balance and water use efficiency of frequently cut *Lolium perenne* L swards at elevated carbon dioxide. *Global Change Biology* 3(3):207-216.

The impact of doubled atmospheric [CO₂] on the carbon balance of regularly cut *Lolium perenne* L. swards was studied for two years under semi-field conditions in the Wageningen Rhizolab. CO₂ and H₂O vapour exchange rates of the swards were measured continuously for two years in transparent enclosures. The light utilization efficiencies of the swards ranged between 1.5 g CO₂ MJ⁻¹ global radiation (high light, ambient [CO₂]) and 2.8 g CO₂ MJ⁻¹ (low light, doubled [CO₂]). The above-ground net primary productivity (NPP) in the enclosures was greater by 29% in 1994 and 43% in 1995 in the doubled [CO₂] treatments, but only 20% and 25% more carbon was recovered in the periodical cuts. Thus, NPP increased significantly more than did the harvested aboveground biomass. The positive [CO₂] effect on net carbon assimilation is therefore associated with a preferential allocation of extra carbon to the roots and soil. In addition to higher canopy photosynthesis and leaf elongation rates, a small part of the positive [CO₂] effects on NPP could be attributed to a decrease of the specific respiration of the shoots. On a canopy basis however, respiration was equal or slightly higher at doubled [CO₂] due to the higher amount of standing biomass. Comparison of NPP and carbon recovered in different harvests showed that allocation to roots and soil was highest in spring, it was low in early summer and increased again in late summer and autumn. The total gross amount of carbon partitioned to the roots and soil during the two year period was 57% more at doubled [CO₂]. The total amount of carbon that was sequestered in the soil after subtraction of the respiratory losses was 458 g m⁻² and 779 g m⁻² in the ambient and doubled [CO₂] treatments, respectively. The average water use efficiency (WUE) of the swards was increased by a factor 1.5 at doubled [CO₂]. Both WUE and its positive interaction with [CO₂] varied between years and were positively correlated with global irradiance. At doubled [CO₂], the higher WUE was fully compensated for by a higher leaf area index. Therefore, total transpiration on a canopy basis was equal for the ambient and the doubled [CO₂] concentrations in both years.

KEYWORDS: ATMOSPHERIC CO₂, BIOSPHERE, CONDUCTANCE, CYCLE, GRASSLAND, IMPACT, PHOTOSYNTHESIS, RESPIRATION, RYEGRASS, TEMPERATURE

2140

Schapendonk, A.H.C.M., W. Stol, D.W.G. van Kraalingen, and B.A.M. Bouman. 1998. LINGRA, a sink/source model to simulate grassland productivity in Europe. *European Journal of Agronomy* 9(2-3):87-100.

A simulation model for the prediction of the productivity of *Lolium perenne* L. grasslands is described and validated. Simulated key processes are light utilization, leaf formation, leaf elongation, tillering, and carbon partitioning (storage, shoot, root). Source- and sink-limited growth are simulated independently. Sink-limited growth is characterized by temperature-dependent leaf expansion and tiller development, whereas source-limited growth is determined by photosynthetic light-use-efficiency of the canopy and the remobilization of stored carbohydrates in the stubble. At each integration step, commonly 1 day, the available amount of carbon from the source is compared with the carbon required by the sink. The actual growth is determined by the minimum value of either the sink or the source. If the source is in excess of the sink, the surplus is allocated to storage carbohydrates in the stubble. This storage carbon is available for remobilization at times that the sink requires more carbohydrates than are available from photosynthesis. In contrast to previous grassland models, LINGRA describes regrowth after defoliation in a mechanistic way, balanced by temperature-driven remobilization of stored carbohydrates. In order to validate LINGRA, an extensive set of experimental data was used, derived from measurements at 35 sites in Europe. The average error between the observed and predicted yields was 14% at the level of irrigated, and 19% at the level of non-irrigated, treatments for the whole of Europe. (C) 1998 Elsevier Science B.V. All rights reserved.

KEYWORDS: CARBON BALANCE, CLIMATE, CO₂- ENRICHMENT, EFFICIENCY, GROWTH, SENESCENCE, SWARD, TEMPERATURE INCREASE, WATER

2141

Schappi, B. 1996. Growth dynamics and population development in an alpine grassland under elevated CO₂. *Oecologia* 106(1):93-99.

Leaf expansion, population dynamics and reproduction under elevated CO₂ were studied for two dominant and four subdominant species in a high alpine grassland (2500 above sea level, Swiss Central Alps). Plots of alpine heath were exposed to 335 $\mu\text{mol l}^{-1}$ and 680 $\mu\text{mol l}^{-1}$ CO₂ in open-top chambers over three growing seasons. Treatments also included natural and moderately improved mineral nutrient supply (40 kg N ha⁻¹ year⁻¹ in an NPK fertilizer mix). Seasonal dynamics of leaf expansion, which was studied for the dominant graminoid *Carex curvula* only, were not affected by elevated CO₂ during two warm seasons or during a cool season. Improved nutrient supply increased both the expansion rate and the duration of leaf growth but elevated CO₂ did not cause any further stimulation. Plant and tiller density (studied in all species) increased under elevated CO₂ in the codominant *Leontodon helveticus* and the subdominant *Trifolium alpinum*, remained unchanged in two other minor species *Poa alpina* and *Phyteuma globulariifolium*, and decreased in *Carex curvula*. In *Potentilla aurea* elevated CO₂ compensated for a natural decline in shoot number. By year 3 the number of fertile shoots in *Leontodon* and individual seed weight in *Carex* were slightly increased under elevated CO₂, indicating CO₂ effects on sexual reproduction in these two dominant species. The results suggest that the effects of elevated CO₂ on the population dynamics of the species studied were not general, but species-specific and rather moderate effects. However, the reduction of tiller density in *Carex*

curvula, in contrast to the increases observed in *Leontodon helveticus* and *Trifolium alpinum*, indicates that elevated CO₂ may negatively affect the abundance of the species most characteristic of this alpine plant community.

KEYWORDS: ANNUALS, CARBON DIOXIDE, PLANT, REPRODUCTION, TEMPERATURE, TUSsock TUNDRA, WHITE CLOVER

2142

Schappi, B., and C. Korner. 1996. Growth responses of an alpine grassland to elevated CO₂. *Oecologia* 105(1):43-52.

Alpine plant species have been shown to exhibit a more pronounced increase in leaf photosynthesis under elevated CO₂ than lowland plants. In order to test whether this higher carbon fixation efficiency will translate into increased biomass production under CO₂ enrichment we exposed plots of narrow alpine grassland (Swiss Central Alps, 2470 m) to ambient (355 $\mu\text{mol l}^{-1}$) and elevated (680 $\mu\text{mol l}^{-1}$) CO₂ concentration using open top chambers. Part of the plots received moderate mineral nutrient additions (40 kg ha⁻¹ year⁻¹) of nitrogen in a complete fertilizer mix). Under natural nutrient supply CO₂ enrichment had no effect on biomass production per unit land area during any of the three seasons studied so far. Correspondingly, the dominant species *Carex curvula* and *Leontodon helveticus* as well as *Trifolium alpinum* did not show a growth response either at the population level or at the shoot level. However, the subdominant generalistic species *Poa alpina* strongly increased shoot growth (+47%). Annual root production (in ingrowth cores) was significantly enhanced in *C. curvula* in the 2nd and 3rd year of investigation (+43%) but was not altered in the bulk samples for all species. Fertilizer addition generally stimulated above-ground (+48%) and below-ground (+26%) biomass production right from the beginning. Annual variations in weather conditions during summer also strongly influenced above-ground biomass production (19-27% more biomass in warm seasons compared to cool seasons). However, neither nutrient availability nor climate had a significant effect on the CO₂ response of the plants. Our results do not support the hypothesis that alpine plants, due to their higher carbon uptake efficiency, will increase biomass production under future atmospheric CO₂ enrichment, at least not in such late successional communities. However, as indicated by the response of *P. alpina*, species-specific responses occur which may lead to altered community structure and perhaps ecosystem functioning in the long-term. Our findings further suggest that possible climatic changes are likely to have a greater impact on plant growth in alpine environments than the direct stimulation of photosynthesis by CO₂. Counter-intuitively, our results suggest that even under moderate climate warming or enhanced atmospheric nitrogen deposition positive biomass responses to CO₂ enrichment of the currently dominating species are unlikely.

KEYWORDS: AMBIENT, ATMOSPHERIC CARBON-DIOXIDE, BALANCE, NITROGEN, PLANT GROWTH, TEMPERATURE, TUSsock TUNDRA, WHITE CLOVER

2143

Schappi, B., and C. Korner. 1997. In situ effects of elevated CO₂ on the carbon and nitrogen status of alpine plants. *Functional Ecology* 11(3):290-299.

1. The effect of elevated CO₂ on tissue composition in an alpine grassland (Swiss Central Alps, 2500m) under both natural and increased nutrient supply (NPK) is summarized. 2. During 3 years of CO₂ enrichment the concentration of total non- structural carbohydrates (TNC) in leaves increased by 32% in *Leontodon helveticus* (largely sugar) and by 56% in *Trifolium alpinum* (largely starch) but did not

change significantly in the dominant sedge *Carex curvula* and in *Poa alpina*, currently a rare species at this site. 3. Enhanced mineral nutrient supply (unlike elevated CO₂) greatly stimulated growth but did not reduce the CO₂-induced TNC accumulation. 4. Under elevated CO₂ nitrogen concentrations (per g TNC-free dry matter) of green leaves decreased in *Leontodon* (-21%) and in *Trifolium* (-24%) but not or only slightly in *Carex* and in *Pea*. NPK addition compensated this CO₂ effect on a nitrogen concentration in *Trifolium* but not in the other species. 5. In below-ground tissue neither TNC nor nitrogen concentration responded to CO₂ fertilization. 6. The nitrogen pool per unit land area at peak season biomass remained unaffected by the CO₂ treatment. 7. Overall our results suggest that the late successional dominant sedge *Carex curvula* remains unaffected by elevated CO₂, independently of mineral nutrient supply, whereas the co-dominant and sub-dominant forbs *Leontodon helveticus* and *Trifolium alpinum* show both an increase of TNC as well as N depletion under elevated CO₂. 8. None of these changes in active plant tissue translate into compositional changes in naturally senesced litter suggesting caution with predictions of CO₂ effects on decomposition based on data from green plant material.

KEYWORDS: ACCUMULATION, ATMOSPHERIC CO₂, DIOXIDE, ESTUARINE MARSH, GROWTH, HIGH-ALTITUDES, LONG-TERM EXPOSURE, LOW-TEMPERATURE, PHOTOSYNTHETIC INHIBITION, TUSsock TUNDRA

2144

Schenk, U., H.J. Jager, and H.J. Weigel. 1996. Nitrogen supply determines responses of yield and biomass partitioning of perennial ryegrass to elevated atmospheric carbon dioxide concentrations. *Journal of Plant Nutrition* 19(10-11):1423-1440.

Perennial ryegrass (*Lolium perenne* L. cv. Parcour) grown at eight levels of nitrogen (N) fertilization (0-765 mg/pot) was exposed to ambient (390 ppm) and elevated (690 ppm) carbon dioxide (CO₂) concentrations for 83 days. Plants were cut three times and dry matter yields determined for each harvest. At final harvest, dry weight of root and stubble biomass was determined, as N concentrations of all plant fractions were determined. Carbon dioxide enrichment effects on yield and total plant biomass increased with increasing N fertilization. The weaker CO₂-related yield enhancement at low N supply was due to the plants inability to increase tiller number. Root fraction of total plant biomass at final harvest was increased by high CO₂ and decreased by N supply. Root biomass was significantly increased by CO₂ enrichment and for both CO₂ treatments the N supply for maximum root mass coincided with the N supply for reaching maximum total plant biomass. A significant correlation between root fraction of total plant dry matter and N concentration of total plant biomass, which was not changed by CO₂ enrichment, indicates that biomass partitioning between shoot and root is controlled by the internal N status of the plant.

KEYWORDS: CO₂-ENRICHMENT, GRASSLANDS, GROWTH-RESPONSE, MOBILIZATION, PLANT-RESPONSES, ROOTS, SOIL, STORAGE, STUBBLE, WHITE CLOVER

2145

Schenk, U., H.J. Jager, and H.J. Weigel. 1997. The response of perennial ryegrass white clover mini-swards to elevated atmospheric CO₂ concentrations: effects on yield and fodder quality. *Grass and Forage Science* 52(3):232-241.

In order to assess the effects of future elevated atmospheric CO₂ concentrations on yield, mineral content and the nutritive value of mixed swards of perennial ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.), both species were grown as monocultures and as different mixtures and were exposed season-long to ambient (380 p.p.m.) and elevated (670 p.p.m.) CO₂ concentrations in open-top

chambers. Mini-swards were cut four times at about monthly intervals at a height of 5 cm, dry-matter yields were determined and content of macrolelements (N, P, K, S, Mg, Ca, Na) and crude fibre, crude protein and ash content were measured. The CO₂-related increase in seasonal yield amounted to 16-38% for white clover monocultures, 12-29% for mixed swards and 5-9% for ryegrass monocultures. The white clover content of all swards was significantly enhanced by elevated CO₂. The K and Na content of total yield was decreased by high CO₂ but did not fall below the minimum requirements for ruminants. As the Ca content of total yield was increased by elevated CO₂ and the P content was not changed, the Ca/P ratio of total yield was increased and exceeded values required for animal nutrition. The crude protein content of total yield was reduced by high CO₂ at the beginning of the growing season only and was increased by elevated CO₂ in the course of the experiment, whereas crude fibre content was decreased through out the season, sometimes falling below the minimum requirement for ruminants. Removal of N, P, S, Mg and Ca by cutting was significantly enhanced because of CO₂ enrichment. The results show that, besides the positive effect of rising atmospheric CO₂ on dry-matter yield of white clover/ryegrass swards, impacts on the nutritive value should be expected. Possible changes in species composition and implications for grassland management are briefly discussed.

KEYWORDS: CARBON DIOXIDE, CLIMATE CHANGE, ENRICHMENT, GROWTH-RESPONSE, LOLIUM-PERENNE, NITROGEN, PASTURE TURVES, PLANT-RESPONSES, SIMULATED SEASONAL-CHANGES, TRIFOLIUM-REPENS

2146

Schenk, U., H.J. Jager, and H.J. Weigel. 1997. The response of perennial ryegrass/white clover swards to elevated atmospheric CO₂ concentrations. 1. Effects on competition and species composition and interaction with N supply. *New Phytologist* 135(1):67-79.

The effects of long-term carbon dioxide enrichment on competition for nutrients and light in a ryegrass/clover association were determined for simulated swards of perennial ryegrass (*Lolium perenne* L. cv. Parcour) and white clover (*Trifolium repens* L. cv. Karina), which were grown as monocultures and in three mixtures (25/75, 50/50, 75/25), according to the replacement design, at two levels of nitrogen (N) supply (no additional N and 200 kg N ha⁻¹) and at season-long ambient (380 ppm) and elevated (670 ppm) CO₂ concentrations, in open-top chambers. Stands were cut four times, at about monthly intervals, to a height of 5 cm. Plant material was separated into different species, fresh and dry weights were determined and the content of macrolelements (N, P, K, S, Mg) in both species was measured. In addition, plant height of both species at harvest dates and during several regrowth periods was monitored. Results indicate that both species made demand on different resources and profited from growth in a mixed sward. CO₂-related yield increase amounted to 16-42% for white clover whereas the effect of high CO₂ on ryegrass yield ranged between -33% and +9% depending on N supply, mixture and year. As a result the contribution of white clover to total yield in mixed swards was significantly enhanced by CO₂ enrichment at many harvests in both N supply treatments. Without additional N supply, shoot competition for light was intensified by CO₂ enrichment to the disadvantage of ryegrass, since clover petioles grew longer and ryegrass was shorter at elevated CO₂. With N fertilization, no marked effect of CO₂ enrichment on interspecific competition could be observed. Since clover and total yield were increased by CO₂ enrichment, nutrient requirements were also increased and potassium deficiency and increased intraspecific competition of clover for K was observed in the mixtures under elevated CO₂ which had the highest nutrient withdrawal. Although white clover profited much more from CO₂ enrichment in both N fertilization treatments, the suppression of ryegrass in mixed swards could only be observed under low N conditions. Generally, the effect of N fertilization on competitive interference between both species was much greater than the effect of

CO₂ enrichment and it is suggested that the effect of elevated CO₂ on the balance of species and the outcome of competition in a grass/clover sward is mainly dependent on the N status.

KEYWORDS: CARBON DIOXIDE, GROWTH-RESPONSE, *LOLIUM-PERENNE*, MINERAL NUTRITION, MODEL-ECOSYSTEMS, PASTURE TURVES, PLANT-RESPONSES, SIMULATED SEASONAL-CHANGES, *TRIFOLIUM-REPENS* L, WHITE CLOVER

2147

Schenk, U., R. Manderscheid, J. Hugen, and H.J. Weigel. 1995. Effects of CO₂ enrichment and intraspecific competition on biomass partitioning, nitrogen-content and microbial biomass carbon in soil of perennial ryegrass and white clover. *Journal of Experimental Botany* 46(289):987-993.

Seedlings of perennial ryegrass (*Lolium perenne* L. cv. Parcour) and white clover (*Trifolium repens* L. cv. Karina) grown at five different plant densities were exposed to ambient (390 ppm) and elevated (690 ppm) CO₂ concentrations. After 43 d the effects of CO₂ enrichment and plant density on growth of shoot and root, nitrogen concentration of tissue, and microbial biomass carbon (C-mic) in soil were determined. CO₂ enrichment of *Lolium perenne* increased shoot growth on average by 17% independent of plant density, while effects on root biomass ranged between -4% and +107% due to an interaction with plant density. Since tiller number per plant was unaffected by elevated CO₂, the small response of shoot growth to CO₂ enrichment was attributed to low sink strength. A significant correlation between nitrogen concentration of total plant biomass and root fraction of total plant dry matter, which was not changed by CO₂ enrichment, indicates that nitrogen status of the plant controls biomass partitioning and the effect of CO₂ enrichment on root growth. Effects of elevated CO₂ and plant density on shoot and root growth of *Trifolium repens* were not significantly interacting and mean CO₂ related increase amounted to 29% and 66%, respectively. However, growth enhancement due to elevated CO₂ was strongest when leaf area index was lowest. Total amounts of nitrogen in shoots and roots were bigger at 690 ppm than at 390 ppm CO₂. There was a significant increase in C-mic in experiments with both species whereas plant density had no substantial effect.

KEYWORDS: DIOXIDE CONCENTRATION, ELEVATED ATMOSPHERIC CO₂, ENVIRONMENTS, GROWTH, LEAF, PHOTOSYNTHESIS, PLANT, RESPIRATION, TEMPERATURE, *TRIFOLIUM-REPENS*

2148

Scherzer, A.J., J. Rebbeck, and R.E.J. Boerner. 1998. Foliar nitrogen dynamics and decomposition of yellow-poplar and eastern white pine during four seasons of exposure to elevated ozone and carbon dioxide. *Forest Ecology and Management* 109(1-3):355-366.

Yellow-poplar (*Liriodendron tulipifera* L.) and eastern white pine (*Pinus strobus* L.) seedlings growing in two plantations were fumigated from 1992 to 1995 in open-top chambers with charcoal-filtered air (CF), ambient air (chamberless), one time ambient ozone (1X), twice ambient ozone (2X), or twice ambient ozone+twice ambient CO₂ (2X+CO₂). Across all treatments and years, concentrations of foliar nitrogen (N) in yellow-poplar averaged 26.3 mg g⁻¹ in June and decreased to 13.8 mg g⁻¹ just prior to leaf senescence. While leaves from all treatments exhibited similar seasonal reductions, actual N concentrations were greatly affected by treatment. Ozone (O-3) alone did not significantly alter foliar N concentrations; however, 2X+CO₂ decreased N concentrations by 18-40% depending on time of sampling. After one season of fumigation, 2X+CO₂-exposed leaves of yellow-poplar decayed significantly more slowly than leaves from all other treatments. In contrast, white pine needles demonstrated few differences in N

concentrations or decomposition during the first 3 years of fumigation. By the fourth season, 2X-CO₂-air significantly reduced N concentrations of current year needles. In needles grown in CF air N concentrations ranged from 14.8 mg g⁻¹ in June to 17.2 mg g⁻¹ in October. 2X+CO₂-air reduced N levels in white pine by 10- 23% depending on time of sampling. For both species, significant differences in N due to leaf age and canopy position must be taken into consideration when evaluating the data. Our experiments indicate that elevated CO₂ in the presence of elevated O-3 can reduce foliar N concentrations and reduce litter decay, thus affecting nutrient cycling. (C) 1998 Elsevier Science B.V.

KEYWORDS: CLIMATE CHANGE, CO₂, FIELD, GROWTH, L SEEDLINGS, LEAF LITTER, NUTRITION, PLANTS, SIMULATED ACID-RAIN, *SPRUCE PICEA-ABIES*

2149

Schier, G.A., and C.J. McQuattie. 1998. Effects of carbon dioxide enrichment on response of mycorrhizal pitch pine (*Pinus rigida*) to aluminum: growth and mineral nutrition. *Trees-Structure and Function* 12(6):340-346.

Carbon dioxide enrichment may increase the Al tolerance of trees by increasing root growth, root exudation and/or mycorrhizal colonization. The effect of elevated CO₂ on the response of mycorrhizal pitch pine (*Pinus rigida* Mill.) seedlings to Al was determined in two experiments with different levels of nutrients, 0.1- or 0.2-strength Clark solution. During each experiment, seedlings inoculated with the ectomycorrhizal fungus *Pisolithus tinctorius* (Pers.) Coker & Couch were grown 13 weeks in sand irrigated with nutrient solution (pH 3.8) containing 0, 6.25, 12.5, or 25 mg/l Al (0, 232, 463, or 927 µM Al) in growth chambers fumigated with 350 (ambient) or 700 (elevated) µl/l CO₂. At ambient CO₂ in the absence of Al, mean total dry weights (DW) of seedlings at the high nutrient level were 164% higher than those at the low level. Total DW at elevated CO₂, in the absence of Al, was significantly greater than that in ambient CO₂ at the low (+34%) and high (+16%) nutrient levels. Root and shoot DW at both nutrient levels decreased with increasing Al concentrations with Al reducing root growth more than shoot growth. Although visible symptoms of Al toxicity in roots and needles were reduced by CO₂ enrichment, there were no significant CO₂ x Al interactions for shoot or root DW. The percentage of seedling roots that became mycorrhizal was negatively related to nutrient level and was greater at elevated than at ambient CO₂ levels. Generally, elevated CO₂ had little effect on concentration of mineral nutrients in roots and needles. Aluminum reduced concentrations of most nutrients by inhibiting uptake.

KEYWORDS: ATMOSPHERIC CO₂ ENRICHMENT, COLONIZATION, ELEVATED CO₂, NUTRIENT, PHOSPHORUS, *PICEA-RUBENS*, *QUERCUS-ALBA*, ROOTS, SEEDLING GROWTH, SOIL N

2150

Schimel, D.S. 1995. Terrestrial biogeochemical cycles - global estimates with remote-sensing. *Remote Sensing of Environment* 51(1):49-56.

The carbon and nitrogen cycles are crucial for understanding the changing Earth system, influencing atmospheric concentrations of greenhouse gases, primary productivity of the biosphere, and biogenic emissions of reactive trace species. The carbon budget of the terrestrial biosphere has attracted special attention because of its role in atmospheric changes in carbon dioxide. The terrestrial biosphere influences atmospheric CO₂ through three main modes: First, large, nearly balanced fluxes of CO₂ in photosynthesis and respiration exhibit a degree of interannual variability which can influence atmospheric CO₂, at least on annual to decadal time scales. Second, land use changes release CO₂ to the atmosphere. Third, poorly understood processes are

likely resulting in enhanced uptake of CO₂ in certain ecosystems, acting as a sink in the global carbon cycle. This sink may result from forest demographics, atmospheric N deposition, or direct CO₂ fertilization, or some synergistic combination of those processes. Global estimates of terrestrial carbon cycle components requires the use of remote observations; however, the appropriate remote sensing strategies are quite different for the various components.

KEYWORDS: ATMOSPHERIC CO₂, BIOSPHERE, CARBON DIOXIDE, FOREST ECOSYSTEMS, HIGH-RESOLUTION RADIOMETER, MODEL, NITROGEN, PHOTOSYNTHESIS, STOMATAL CONDUCTANCE, TALLGRASS PRAIRIE

2151

Schimel, D.S. 1995. Terrestrial ecosystems and the carbon-cycle. *Global Change Biology* 1(1):77-91.

The terrestrial biosphere plays an important role in the global carbon cycle. In the 1994 Intergovernmental Panel Assessment on Climate Change (IPCC), an effort was made to improve the quantification of terrestrial exchanges and potential feedbacks from climate, changing CO₂, and other factors; this paper presents the key results from that assessment, together with expanded discussion. The carbon cycle is the fluxes of carbon among four main reservoirs: fossil carbon, the atmosphere, the oceans, and the terrestrial biosphere. Emissions of fossil carbon during the 1980s averaged 5.5 Gt C y⁻¹. During the same period, the atmosphere gained 3.2 Gt C y⁻¹, and the oceans are believed to have absorbed 2.0 Gt C y⁻¹. The regrowing forests of the Northern Hemisphere may have absorbed 0.5 Gt C y⁻¹ during this period. Meanwhile, tropical deforestation is thought to have released an average 1.6 Gt C y⁻¹ over the 1980s. While the fluxes among the four pools should balance, the average 1980s values lead to a 'missing sink' of 1.4 Gt C y⁻¹. Several processes, including forest regrowth, CO₂ fertilization of plant growth (c. 1.0 Gt C y⁻¹), N deposition (c. 0.6 Gt C y⁻¹), and their interactions, may account for the budget imbalance. However, it remains difficult to quantify the influences of these separate but interactive processes. Uncertainties in the individual numbers are large, and are themselves poorly quantified. This paper presents detail beyond the IPCC assessment on procedures used to approximate the flux uncertainties. Lack of knowledge about positive and negative feedbacks from the biosphere is a major limiting factor to credible simulations of future atmospheric CO₂ concentrations. Analyses of the atmospheric gradients of CO₂ and (CO₂)-C-13 concentrations provide increasingly strong evidence for terrestrial sinks, potentially distributed between Northern Hemisphere and tropical regions, but conclusive detection in direct biomass and soil measurements remains elusive. Current regional-to-global terrestrial ecosystem models with coupled carbon and nitrogen cycles represent the effects of CO₂ fertilization differently, but all suggest long-term responses to CO₂ that are substantially smaller than potential leaf- or laboratory whole plant-level responses. Analyses of emissions and biogeochemical fluxes consistent with eventual stabilization of atmospheric CO₂ concentrations are sensitive to the way in which biospheric feedbacks are modeled by c. 15%. Decisions about land use can have effects of 100s of Gt C over the next few centuries, with similarly significant effects on the atmosphere. Critical areas for future research are continued measurements and analyses of atmospheric data (CO₂ and (CO₂)-C-13) to serve as large-scale constraints, process studies of the scaling from the photosynthetic response to CO₂ to whole-ecosystem carbon storage, and rigorous quantification of the effects of changing land use on carbon storage.

KEYWORDS: ATMOSPHERIC CARBON, BIOMASS, DIOXIDE, ELEVATED CO₂, FOREST ECOSYSTEMS, GLOBAL CLIMATE-CHANGE, GROWTH-RESPONSE, NITROGEN DEPOSITION, STORAGE, TREE GROWTH

2152

Schindler, D.W., and S.E. Bayley. 1993. The biosphere as an increasing sink for atmospheric carbon - estimates from increased nitrogen deposition. *Global Biogeochemical Cycles* 7(4):717-733.

Estimates of carbon uptake and storage based on global nitrogen deposition, C:N ratios for typical terrestrial ecosystems, and recent ecosystem-scale nutrient studies indicate that 1.0-2.3 Gt C yr⁻¹ of carbon storage may be stimulated by anthropogenically caused increases in nitrogen deposition in the past century. Sixty four to eighty four percent of global nitrogen uptake appears to occur on northern continents, with the remainder largely in northern coastal oceans. Increased nitrogen input by terrestrial ecosystems causes increased accumulation of carbon as plant tissue, with C:N ratios generally 50 to 200:1. Calculations suggest that northern continents are a major sink for carbon and that nitrogen-stimulated carbon uptake may more or less balance global carbon losses to the atmosphere from deforestation and agriculture. Much of the uptake appears to occur in aggrading forests, and the question of how long it can continue has important consequences for global carbon budgets.

KEYWORDS: ACIDIFICATION, BUDGET, CO₂, CYCLE, DECOMPOSITION, ECOSYSTEMS, FOREST, GLOBAL CHANGE, OCEANIC UPTAKE, SPHAGNUM

2153

Schlesinger, W.H. 1993. Response of the terrestrial biosphere to global climate change and human perturbation. *Vegetatio* 104:295-305.

Despite 20 years of intensive effort to understand the global carbon cycle, the budget for carbon dioxide in the atmosphere is unbalanced. To explain why atmospheric CO₂ is not increasing as rapidly as it should be, various workers have suggested that land vegetation acts as a sink for carbon dioxide. Here, I examine various possibilities and find that the evidence for a sink of sufficient magnitude on land is poor. Moreover, it is unlikely that the land vegetation will act as a sink in the postulated warmer global climates of the future. In response to rapid human population growth, destruction of natural ecosystems in the tropics remains a large net source of CO₂ for the atmosphere, which is only partially compensated by the potential for carbon storage in temperate and boreal regions. Direct and inadvertent human effects on land vegetation might increase the magnitude of regional CO₂ storage on land, but they are unlikely to play a significant role in moderating the potential rate of greenhouse warming in the future.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, ELEVATED CO₂, FOREST ECOSYSTEMS, LAND-USE, NITROGEN, NO-TILLAGE, ORGANIC-CARBON, SOIL PROPERTIES, STORAGE, TUSsock TUNDRA

2154

Schmid, R., R. Forster, and M.J. Dring. 1992. Circadian-rhythm and fast responses to blue-light of photosynthesis in ectocarpus (phaeophyta, ectocarpales) .2. Light and co₂ dependence of photosynthesis. *Planta* 187(1):60-66.

Photosynthesis of *Ectocarpus siliculosus* (Dillwyn) Lyngb. under continuous saturating red irradiation follows a circadian rhythm. Blue-light pulses rapidly stimulate photosynthesis with high effectiveness in the troughs of this rhythm but the effectiveness of such pulses is much lower at its peaks. In an attempt to understand how blue light and the rhythm affected photosynthesis, the effects of inorganic carbon on photosynthetic light saturation curves were studied under different irradiation conditions. The circadian rhythm of photosynthesis was apparent only at irradiances which were not limiting for photosynthesis. The same was found for blue-light-stimulated photosynthesis, although

stimulation was observed also under very low red-light irradiances after a period of adaptation, provided that the inorganic-carbon concentration was not in excess. Double-reciprocal plots of light-saturated photosynthetic rates versus the concentration of total inorganic carbon (up to 10 mM total inorganic carbon) were linear and had a common constant for half-saturation (3.6 mM at pH 8) at both the troughs and the peaks of the rhythm and before and after blue-light pulses. Only at very low carbon concentrations was a clear deviation found from these lines for photosynthesis at the rhythm maxima (red and blue light), which indicated that the strong carbon limitation specifically affected photosynthesis at the peak phases of the rhythm. Very high inorganic carbon concentrations (20 mM) in the medium diminished the responses to blue light, although they did not fully abolish them. The kinetics of the stimulation indicate that the rate of photosynthesis is affected by two blue-light-dependent components with different time courses of induction and decay. The faster component seemed to be at least partially suppressed at red-light irradiances which were not saturating for photosynthesis. Lowering the pH of the medium had the same effects as an increase of the carbon concentration to levels of approx. 10 mM. This indicates that *Ectocarpus* takes up free CO₂ only and not bicarbonate, although additional physiological mechanisms may enhance the availability of CO₂.

KEYWORDS: CHLAMYDOMONAS-SEGNIS, DIOXIDE, INORGANIC CARBON-SOURCES

2155

Schmitt, V., A. Kussmaul, and A. Wild. 1999. Interaction of elevated CO₂ and ozone concentrations and irrigation regimes on leaf anatomy and carbohydrate status of young oak (*Quercus petraea*) trees. *Zeitschrift Fur Naturforschung C-A Journal of Biosciences* 54(9-10):812-823.

Young sessile oak (*Quercus petraea*) trees were exposed for one vegetation period in closed environmental chambers in a crossed factorial study on effects to varied CO₂ concentrations, ozone concentrations and irrigation treatments. Elevated CO₂ concentrations (ambient + 350 μ mol mol⁻¹) caused a significant increase in biomass production, alterations in leaf anatomy and chloroplast ultrastructure as well as an increase in leaf starch content, as compared to ambient CO₂ concentrations. The effects of elevated O₃ concentrations and drought stress were far less distinct. The leaf starch content was influenced by CO₂ and O₃ in a synergistic manner.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO₂, CARBON DIOXIDE, ENRICHMENT, GROWTH, LEAVES, PLANTS, SOURCE-SINK RELATIONS, STARCH, ULTRASTRUCTURE

2156

Schneider, S.H., and T.L. Root. 1996. Ecological implications of climate change will include surprises. *Biodiversity and Conservation* 5(9):1109-1119.

In addition to assessing the impacts of CO₂ doubling on environment and society, more consideration is needed to estimate extreme events or 'surprises'. This is particularly important at the intersection of disciplines like climate and ecology because the potential for large discontinuities is high given all the possible climate/biota interactions. The vast disparities in scales encountered by those working in traditional ecology (typically 20 m) and climatology (typically 200 km) make diagnoses of such interactions difficult, but these can be addressed by an emerging research paradigm we call strategic cyclical scaling (SCS). The need to anticipate outlier events and assign them subjective probabilities suggests emphasis on interdisciplinary research associations. The desire to reduce societal vulnerability to such events suggests the need to build adaptive management and diverse economic activities into social organizations. The effectiveness of adaptation responses to anticipated

climatic changes is complicated when consideration of transient changes, regional disturbances, large unforeseeable natural fluctuations and surprises are considered. Slowing down the rate of disturbances and decreasing vulnerability are advocated as the most prudent responses to the prospect of human-induced climatic changes.

KEYWORDS: CO₂, SCALE

2157

Scholes, M.C., D. Powlson, and G.L. Tian. 1997. Input control of organic matter dynamics. *Geoderma* 79(1-4):25-47.

The amount and quality of inputs into soil organic matter will be altered by both climate and landuse change. The increase in growth of plants caused by increasing CO₂ concentration implies not only potential increases in yields but also increases in plant residues. Simulation models using doubled CO₂ levels predict global net primary productivity (NPP) to increase by 16.3%, over half of which will occur in the tropics. For tropical ecosystems increases in NPP will be dominated by the effects of elevated CO₂, with water and nitrogen availability and temperature playing a less significant role. Phosphorus limitation may determine whether the potential for increased plant growth will be realized. The distribution of C₃ and C₄ species in the tropics could be affected by landuse change and estimates of yield increases will be dependent on their proportions. The allocation of photosynthate to the root will increase under elevated CO₂, resulting in increased fine root dry weight and root length. Root sink strength and the turnover of roots and associated symbionts are critical knowledge gaps. Carbon:nitrogen ratios in tissues will increase resulting in decreased decomposition rates. The concentration of secondary compounds will be affected more by nitrogen limitations than a direct CO₂ effect. Changes in lignin, tannin and polyphenol levels are more important in the decomposability of tropical liners than changes in the C:N ratios. Decomposition models will have to be altered to take into account changes in plant composition. The role of models in predicting the effects of management practice on long-term fertility is addressed. (C) 1997 Elsevier Science B.V.

KEYWORDS: ATMOSPHERIC CO₂ ENRICHMENT, C-13 NATURAL ABUNDANCE, CHEMICAL-COMPOSITION, ELEVATED CARBON-DIOXIDE, NITROGEN MINERALIZATION, NUTRIENT RELEASE, ROOT-GROWTH, SIZE-FRACTIONS, SOIL MICROBIAL BIOMASS, TROPICAL CONDITIONS

2158

Scholes, R.J., and N. vanBreemen. 1997. The effects of global change on tropical ecosystems. *Geoderma* 79(1-4):9-24.

Alteration of land use will continue to be the dominant driver of environmental change in the tropics for the next several decades. It can take the form of fundamental vegetation cover transformation, or of intensification of existing land use without substantial change in cover type. Atmospheric composition changes and resultant climate changes could become ecologically significant within the next century. Changes in atmospheric composition in the tropics are essentially the same as those in higher latitudes, despite differences in the source and sink strengths for trace gases. Such changes can affect the functioning of tropical ecosystems through several processes, principally those related to carbon and nutrient assimilation and their interactions. Atmospheric composition may also have an indirect affect on tropical ecosystems via its effects on the climate. Predicted temperature increases in the tropics are less extreme than at high latitudes, but could still be biologically significant, especially at the tropical margins. The structure and productivity of ecosystems of the subhumid and dry tropics are very sensitive to changes in water balance, which could be caused by a combination of changes in precipitation and temperature. It is presently not possible to predict rainfall changes at ecologically meaningful scales

with any confidence. (C) 1997 Elsevier Science B.V.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, CLIMATE, CO₂, DECOMPOSITION, DEFORESTATION, GRASSLANDS, MODEL, NITROGEN, SOIL ORGANIC MATTER, TURNOVER

2159

Schortemeyer, M., O.K. Atkin, N. McFarlane, and J.R. Evans. 1999. The impact of elevated atmospheric CO₂ and nitrate supply on growth, biomass allocation, nitrogen partitioning and N₂ fixation of *Acacia melanoxylon*. *Australian Journal of Plant Physiology* 26(8):737-747.

The interactive effects of nitrate supply and atmospheric CO₂ concentration on growth, N₂ fixation, dry matter and nitrogen partitioning in the leguminous tree *Acacia melanoxylon* R. Br. were studied. Seedlings were grown hydroponically in controlled-environment cabinets for 5 weeks at seven N-15- labelled nitrate levels, ranging from 3 to 6400 mmol m⁻³. Plants were exposed to ambient (similar to 350 μ mol mol⁻¹) or elevated (similar to 700 μ mol mol⁻¹) atmospheric CO₂ for 6 weeks. Total plant dry mass increased strongly with nitrate supply. The proportion of nitrogen derived from air decreased with increasing nitrate supply. Plants grown under either ambient or elevated CO₂ fixed the same amount of nitrogen per unit nodule dry mass (16.6 mmol N per g nodule dry mass) regardless of the nitrogen treatment. CO₂ concentration had no effect on the relative contribution of N₂ fixation to the nitrogen yield of plants. Plants grown with greater than or equal to 50 mmol m⁻³ N and elevated CO₂ had approximately twice the dry mass of those grown with ambient CO₂ after 42 days. The rates of net CO₂ assimilation under growth conditions were higher per unit leaf area for plants grown under elevated CO₂. Elevated CO₂ also decreased specific foliage area, due to an increase in foliage thickness and density. Dry matter partitioning between plant organs was affected by ontogeny and nitrogen status of the plants, but not by CO₂ concentration. In contrast, plants grown under elevated CO₂ partitioned more of their nitrogen to roots. This could be attributed to reduced nitrogen concentrations in foliage grown under elevated CO₂.

KEYWORDS: ALNUS-GLUTINOSA, CARBON DIOXIDE, DYNAMICS, ECOSYSTEMS, ENRICHMENT, GAS-EXCHANGE, MODULATION, PLANTAGO-MAJOR, SEEDLINGS, TRIFOLIUM-REPENS L

2160

Schortemeyer, M., U.A. Hartwig, G.R. Hendrey, and M.J. Sadowsky. 1996. Microbial community changes in the rhizospheres of white clover and perennial ryegrass exposed to free air carbon dioxide enrichment (FACE). *Soil Biology and Biochemistry* 28(12):1717-1724.

Increases in the global atmospheric concentration of CO₂ will not only directly affect the growth of plants, but might also alter the living conditions for soil biota. This could lead to shifts in the size and composition of the soil microbial communities. In this study we investigated the response of heterotrophic bacteria, NH₄⁺-oxidising bacteria, and *Rhizobium leguminosarum* by. *trifolii* populations to elevated atmospheric CO₂ concentrations in a model field-scale grassland ecosystem. The Free Air CO₂ Enrichment (FACE) facility in Eschikon, Switzerland, releases CO₂-enriched air into three large circular areas, each of 18 m dia, to a final CO₂ concentration of 600 μ mol mol⁻¹, while three control areas of the same size receive ambient CO₂ concentrations (similar to 350 μ mol mol⁻¹). For this study, white clover (*Trifolium repens* L.) and perennial ryegrass (*Lolium perenne* L.) were grown as replicated monocultures within the FACE rings. Soil samples were taken from 0-10 cm depth in May and November 1994 (the second year of CO₂-enrichment), and rhizosphere soil was obtained from clover and ryegrass roots for enumeration of bacteria. While the total numbers of culturable heterotrophic bacteria (determined by plate counts) in the rhizospheres of both plant species

were little affected by CO₂-enrichment, the populations of *R. leguminosarum* by. *trifolii* (enumerated by MPN) were increased two-fold in the rhizospheres of white clover exposed to elevated atmospheric CO₂. There was no effect of the CO₂ concentration on the populations of *R. leguminosarum* by. *trifolii* in the rhizospheres of perennial ryegrass, indicating that the increase of *Rhizobium* numbers is a host-related response to elevated atmospheric CO₂. The numbers of autotrophic NH₄⁺-oxidizing bacteria in the rhizospheres (enumerated by MPN) were unaffected by the atmospheric CO₂ concentration. There was also no effect of the CO₂ concentration on the amount of microbial biomass C in the bulk, non-rhizosphere soils in white clover or perennial ryegrass plots. These data indicate that under a legume crop, at least in terms of inoculum quality in the rhizosphere soil, symbiotic nitrogen-fixing organisms might be favoured by elevated atmospheric CO₂ concentrations. (C) 1997 Elsevier Science Ltd.

KEYWORDS: ATMOSPHERIC CO₂ ENRICHMENT, BIOMASS-C, COMPETITION, DECOMPOSITION, ELEVATED CO₂, GROWTH, HETEROTROPHIC BACTERIA, LEGUMES, RESPONSES, ROOT

2161

Schrope, M.K., J.P. Chanton, L.H. Allen, and J.T. Baker. 1999. Effect of CO₂ enrichment and elevated temperature on methane emissions from rice, *Oryza sativa*. *Global Change Biology* 5(5):587-599.

Methane emissions from rice grown within Temperature Gradient Greenhouse Tunnels under doubled CO₂ concentrations were 10-45 times less than emissions from control plants grown under ambient CO₂. For two cultivars of rice (cvs. Lemont and IR-72), methane emissions increased with a temperature increase of 2 degrees, from outdoor ambient temperatures to the first cell of the ambient CO₂ tunnel (ambient temperature + 2 degrees C). Within both tunnels and for both cultivars methane emissions decreased with further temperature increases (from 2 degrees to 5 degrees C above ambient). Carbon dioxide enrichment stimulated both above- and below-ground production. Our original hypothesis was that increased CO₂ would stimulate plant productivity and therefore stimulate methane emission, since direct linkages between these parameters have been observed. We hypothesize that CO₂ enrichment led to the attenuation of methane production due to increased delivery of oxygen to the rhizosphere because of increased root biomass and porosity. The increased root biomass due to elevated CO₂ may have more effectively aerated the soil, suppressing methane production. However, this study may be unique because the low organic content (<1%) of the sandy soils in which the rice was grown created very little oxygen demand.

KEYWORDS: ATMOSPHERIC METHANE, BACTERIA, CARBON DIOXIDE, EXCHANGE, GROWTH RATE, METHANOGENESIS, METHYL-FLUORIDE, OXIDATION, SEASONAL-VARIATION, STABLE ISOTOPES

2162

Schulte, M., C. Herschbach, and H. Rennenberg. 1998. Interactive effects of elevated atmospheric CO₂, mycorrhization and drought on long-distance transport of reduced sulphur in young pedunculate oak trees (*Quercus robur* L.). *Plant, Cell and Environment* 21(9):917-926.

Pedunculate oak (*Quercus robur* L.) was germinated and grown under nutrient non-limiting conditions for a total of 10-15 weeks at ambient CO₂ concentration and 1100 μ mol mol⁻¹ CO₂ either in the presence or the absence of the mycorrhizal fungus *Laccaria laccata*. Half of the oak trees of these treatments were exposed to drought during final growth by suspending the water supply for 21 d. Mycorrhization and elevated atmospheric CO₂ each enhanced total plant biomass per tree. Whereas additional biomass accumulation of trees grown under elevated

CO₂ was mainly attributed to increased growth of lateral roots, mycorrhization promoted shoot growth. Water deficiency reduced biomass accumulation without affecting relative water content, but this effect was more pronounced in mycorrhizal as compared to non-mycorrhizal trees. Elevated CO₂ partially prevented the development of drought stress, as indicated by leaf water potential, but did not counteract the negative effects of water deficiency on growth during the time studied. Enhanced biomass accumulation requires adaption in protein synthesis and, as a consequence, enhanced allocation of reduced sulphur produced in the leaves to growing tissues. Therefore, allocation of reduced sulphur from oak leaves was studied by flap-feeding radiolabelled GSH, the main long-distance transport form of reduced sulphur, to mature oak leaves. Export of radiolabel proceeded almost exclusively in basipetal direction to the roots. The rate of export of radioactivity out of the fed leaves was significantly enhanced under elevated CO₂, irrespective of mycorrhization. A higher proportion of the exported GSH was transported to the roots than to basipetal stem sections under elevated CO₂ as compared to ambient CO₂. Mycorrhization did not affect S-35 export out of the fed leaves, but the distribution of radiolabel between stem and roots was altered in preference of the stem. Trees exposed to drought did not show appreciable export of the S-35 radioactivity fed to the leaves when grown under ambient CO₂. Apparently, drought inhibited basipetal transport of reduced sulphur at the level of phloem loading and/or phloem transport. Elevated CO₂ seemed to counteract this effect of drought stress to some extent, since higher leaf water potentials and improved S-35 export out of the fed leaves was observed in oak trees exposed to drought and elevated CO₂ as compared to trees exposed to drought and ambient CO₂.

KEYWORDS: *ABIES KARST L, CARBON DIOXIDE, ENRICHMENT, FAGUS-SYLVATICA, GAS-EXCHANGE, GROWTH, PLANTS, SEEDLINGS, SULFUR NUTRITION, WATER-STRESS*

2163

Schwanz, P., K.H. Haberle, and A. Polle. 1996. Interactive effects of elevated CO₂, ozone and drought stress on the activities of antioxidative enzymes in needles of Norway spruce trees (*Picea abies*, [L.] Karsten) grown with luxurious N- supply. *Journal of Plant Physiology* 148(3-4):351-355.

The aim of the present study was to address the complex interactions of environmental constraints, ozone and drought stress, with elevated atmospheric CO₂ on the activities of antioxidative enzymes and soluble protein contents in needles of Norway spruce trees (*Picea abies* L.). Five-year-old spruce trees were kept from bud break in June until January of the following year in phytochambers under climatic conditions similar to those of a natural site in the Bavarian forest. The trees were well-supplied with nitrogen and exposed to either elevated CO₂ (ambient + 200 µmol L⁻¹), elevated ozone (80 nL L⁻¹), from June to October) or to a combination of both factors. Controls were grown with 20 nL L⁻¹ O₃ and ambient CO₂ levels. In each chamber, a subset of trees was subjected to episodic drought stress in summer. Needles from controls investigated in October (summer conditions) and January (winter conditions) showed little seasonal variation of superoxide dismutase (SOD), an approximately 2-fold reduction in catalase (CAT), and a 2-fold increase in guaiacol peroxidase (POD) activity. Exposure to elevated CO₂ did not affect the activities of any of these enzymes in October and January, respectively, but caused a significant reduction in soluble protein. Ozone had no significant effect. Drought stress caused memory effects. In January, needles from trees drought-stressed in summer contained higher activities of defence enzymes and soluble protein contents than needles from well-watered trees. Three weeks after the end of a drought episode in summer, needles from spruce trees grown at elevated CO₂ contained increased CAT and POD activities as compared to needles from trees grown at ambient CO₂. This response was increased, if elevated ozone was present as an additional stress

factor. These observations suggest that Norway spruce trees grown under elevated atmospheric CO₂ concentrations might better be able to compensate environmental stresses than trees grown at ambient atmospheric CO₂ concentrations.

KEYWORDS: *GAS-EXCHANGE, PLANTS, SUPEROXIDE-DISMUTASE ACTIVITY*

2164

Schwanz, P., B.A. Kimball, S.B. Idso, D.L. Hendrix, and A. Polle. 1996. Antioxidants in sun and shade leaves of sour orange trees (*Citrus aurantium*) after long-term acclimation to elevated CO₂. *Journal of Experimental Botany* 47(305):1941-1950.

Antioxidative systems and the contents of pigments, malondialdehyde, soluble protein, and carbohydrate were investigated in sun- and shade-acclimated leaves of sour orange (*Citrus aurantium*) trees that had been grown for 7.5 years under ambient and elevated (+300 µmol mol⁻¹) atmospheric CO₂ concentrations. Sun-acclimated leaves contained higher ascorbate, glutathione and soluble carbohydrate contents and higher catalase activities than shade-acclimated leaves. The activities of superoxide dismutases, which belonged to the family of Cu/Zn-isozymes, were similar in sun- and shade- acclimated leaves and decreased in response to enhanced CO₂. In shade-acclimated leaves, none of the other parameters studied was affected by elevated CO₂. In sun-acclimated leaves elevated CO₂ caused increases in carbohydrate and ascorbate contents. There was no evidence for enhanced lipid peroxidation as assessed from the determination of the malondialdehyde contents under either conditions.

KEYWORDS: *CARBON-DIOXIDE CONCENTRATIONS, CUZN-SUPEROXIDE, GLUTATHIONE-REDUCTASE, HIGH LIGHT, NEEDLES, NORWAYSPRUCE, PHOTOOXIDATIVE STRESS, PICEA-ABIES L, RISING ATMOSPHERIC CO2, SUPEROXIDE-DISMUTASE*

2165

Schwanz, P., C. Picon, P. Vivin, E. Dreyer, J.M. Guehl, and A. Polle. 1996. Responses of antioxidative systems to drought stress in pendunculate oak and maritime pine as modulated by elevated CO₂. *Plant Physiology* 110(2):393-402.

The aim of the present study was to investigate the effects of an enhanced CO₂ concentration alone or in combination with drought stress on antioxidative systems of a deciduous (oak; *Quercus robur*) and an evergreen (pine; *Pinus pinaster*) tree species. The seedlings were grown for one season in a greenhouse in tunnels supplied with 350 or 700 µmol L⁻¹ CO₂. The experiment was repeated in a second year. Antioxidants, protective enzymes, soluble protein, and pigments showed considerable fluctuations in different years. Elevated CO₂ caused significant reductions in the activities of superoxide dismutases in both oak and pine. The activities of ascorbate peroxidase and catalase were also reduced in most cases. The activities of dehydroascorbate reductase, monodehydroascorbate radical reductase, glutathione reductase, and guaiacol peroxidase were affected little or not at all by elevated CO₂. When the trees were subjected to drought stress by withholding water, the activities of antioxidative enzymes decreased in leaves of pine and oak grown at ambient CO₂ and increased in plants grown at elevated CO₂ concentrations. The present results suggest that growth in elevated CO₂ might reduce oxidative stress to which leaf tissues are normally exposed and enhance metabolic flexibility to encounter increased stress by increases in antioxidative capacity.

KEYWORDS: *ASCORBATE, CLIMATE CHANGE, GLUTATHIONE, LEAVES, NEEDLES, PHASEOLUS-VULGARIS L, PHOTOSYNTHESIS, PICEA-ABIES L, QUERCUS-ROBUR L, WATER-STRESS*

2166

Schwanz, P., and A. Polle. 1998. Antioxidative systems, pigment and protein contents in leaves of adult Mediterranean oak species (*Quercus pubescens* and *Q. ilex*) with lifetime exposure to elevated CO₂. *New Phytologist* 140(3):411-423.

The aim of the present study was to investigate the effects of elevated CO₂ on the antioxidative systems and the contents of pigments, soluble protein and lipid peroxidation in leaves of adult oaks, *Quercus pubescens* and *Quercus ilex*, grown at naturally enriched CO₂ concentrations. For this purpose, a field study was conducted at two CO₂ springs in Central Italy. Measurements of the pre-dawn water potentials indicated less drought stress in trees close to CO₂ springs than in those grown at ambient CO₂ concentrations. Most leaf constituents investigated showed significant variability between sampling dates, species and sites. The foliar contents of protein and chlorophylls were not affected in trees grown close to the CO₂ vents compared with those in ambient conditions. Increases in glutathione and other soluble thiols were observed, but these responses might have been caused by a low pollution of the vents with sulphurous gases. At CO₂ vents, glutathione reductase was unaffected, and superoxide dismutase activity was significantly diminished, in both species. Generally, the activities of catalase, guaiacol peroxidase and ascorbate peroxidase as well as the sum of dehydroascorbate and ascorbate were decreased in leaves from trees grown in naturally CO₂-enriched environments compared with those grown at ambient CO₂ concentrations. The reduction in protective enzymes did not result in increased lipid peroxidation, but increased monodehydroascorbate radical reductase and dehydroascorbate reductase activities found in leaves of *Q. pubescens* suggest that the smaller pool of ascorbate was subjected to higher turnover rates. These data show that changes in leaf physiology persist, even after lifetime exposure to enhanced atmospheric CO₂. The results suggest that the down-regulation of protective systems, which has also previously been found in young trees or seedlings under controlled exposure to elevated CO₂ concentrations, might reflect a realistic response of antioxidative defences in mature trees in a future high-CO₂ world.

KEYWORDS: ASCORBATE, CARBON DIOXIDE, DROUGHT STRESS, ENHANCED OZONE, ENZYMES, NEEDLES, PICEA-ABIES L, RESPONSES, RISING ATMOSPHERIC CO₂, TREES

2167

Schwartz, M.W. 1992. Potential effects of global climate change on the biodiversity of plants. *The Forestry Chronicle* 68(4):462-471.

Climatologists have observed a consistent increase in atmospheric CO₂ over the past 30 years. It is predicted that CO₂ levels could double the pre-industrial level of 280 ppm by the year 2100, perhaps much earlier. Climate models of doubled atmospheric CO₂ predict that mean temperatures will increase between 1.5 and 4.5-degrees-C globally; these temperature changes will be greater at high latitudes. Mid-continental regions will experience lower rainfall. Predictions of species northward range shifts in response to climate change vary from 100 km to over 500 km. Historical evidence of species range movements following the Pleistocene indicate that tree species typically migrated at rates of 10 km to 40 km per century. A simulation model that predicts the migration response of trees through modern fragmented landscapes predicts migration rates much lower than Pleistocene observations. Thus migration response is likely to lag far behind rates of climatic change, potentially threatening narrowly distributed species whose predicted future ranges do not overlap with their current range. Insect pests and microbial pathogens should respond to climatic warming faster than long-lived trees. Predicted increased drought frequency may increase plant stress and thereby increase the frequency of insect outbreaks and disease. Predictions of species responses are complicated by direct effects of increased CO₂, such as increased water-use efficiency. However, response to elevated CO₂ varies among species. Thus, shifts

in composition within plant communities are also likely, but are, as yet, unpredictable.

2168

Scurlock, J.M.O., and D.O. Hall. 1998. The global carbon sink: a grassland perspective. *Global Change Biology* 4(2):229-233.

The challenge to identify the biospheric sinks for about half the total carbon emissions from fossil fuels must include a consideration of below-ground ecosystem processes as well as those more easily measured above-ground. Recent studies suggest that tropical grasslands and savannas may contribute more to the 'missing sink' than was previously appreciated, perhaps as much as 0.5 Pg (= 0.5 Gt) carbon per annum. The rapid increase in availability of productivity data facilitated by the Internet will be important for future scaling-up of global change responses, to establish independent lines of evidence about the location and size of carbon sinks.

KEYWORDS: ATMOSPHERIC CO₂, CLIMATE CHANGE, CONIFEROUS FORESTS, CYCLE, ECOSYSTEMS, PRODUCTIVITY, SOIL CARBON, STORAGE, TEMPERATE, WORLDWIDE

2169

Seaton, K.A., and D.C. Joyce. 1993. Effects of low-temperature and elevated CO₂ treatments and of heat-treatments for insect disinfestation on some native-australian cut flowers. *Scientia Horticulturae* 56(2):119-133.

For bioassay insects, 14 days storage at 1-degrees-C was required for 100% kill of adult flour beetles (*Tribolium confusum* Koch.), and 10 days at 1-degrees-C killed 100% of Mediterranean fruit fly larvae (*Ceratitis capitata* Wied.). A CO₂ enriched atmosphere of between 45% and 60% (11% and 8% O₂, respectively) reduced the time required to achieve 100% mortality of these bioassay insects to 7 days at 1-degrees-C. Increasing the CO₂ content of the atmosphere to 80% (4% O₂) did not further reduce the time to achieve 100% mortality. Vase life of red kangaroo paw (*Anigozanthos rufus*) was reduced below that of the unstored control after just 3.5 days at 1-degrees-C. Geraldton wax (*Chamaelaucium uncinatum*) cultivar 'Newmarracarra' was similarly affected after 14 days, and acorn banksia (*Banksia prionotes*) after 28 days. Vase lives of Geraldton wax cultivar 'Newmarracarra' and of red kangaroo paw were not reduced following 7 days storage at 1-degrees-C in 15% CO₂, compared with controls stored in air. However, Geraldton wax and red kangaroo paw vase lives were shortened and flower colour was altered after storage for 7 days in 30% CO₂ (15% O₂). Geraldton wax and red kangaroo paw had no vase lives following storage in 80% CO₂ (4% O₂) at 1-degrees-C for 3.5 days. Heat treatments of hot water dips (46-degrees-C for 30 min or 56-degrees-C for 10 min) and vapour heat (66-degrees-C for 10 min) killed 100% of adult flour beetles and Mediterranean fruit fly larvae, but damaged and shortened the vase lives of Geraldton wax and banksia.

KEYWORDS: COLD-STORAGE, INFLORESCENCES, TELEPEA-SPECIOSISSIMA, PHYSIOLOGY, PROTEACEAE, QUARANTINE PROCEDURE, VASE LIFE

2170

Seegmuller, S., and H. Rennenberg. 1994. Interactive effects of mycorrhization and elevated carbon-dioxide on growth of young pedunculate oak (*Quercus robur* L.) trees. *Plant and Soil* 167(2):325-329.

Pedunculate oak (*Quercus robur* L.) was germinated and grown at ambient CO₂ level and 650 ppmv CO₂ in the presence and absence of the ectomycorrhizal fungus *Laccaria laccata* for a total of 6 months under

nutrient non-limiting conditions. Mycorrhization and elevated atmospheric CO₂ each supported the growth of the trees. Stem height, stem diameter, and dry matter accumulation of pedunculate oak were increased by mycorrhization. Elevated atmospheric CO₂ enhanced stem height, stem diameter, fresh weight and dry weight, as well as lateral root formation of the trees. In combination, mycorrhization and elevated atmospheric CO₂ had a more than additive, positive effect on tree height and biomass accumulation, and further improved lateral root formation of the trees. From these findings it is suggested that the efficiency of the roots in supporting the growth of the shoot is increased in mycorrhized oak trees at elevated atmospheric CO₂.

KEYWORDS: CO₂- ENRICHMENT, MINERAL NUTRITION, SEEDLINGS

2171

Seegmuller, S., M. Schulte, C. Herschbach, and H. Rennenberg. 1996. Interactive effects of mycorrhization and elevated atmospheric CO₂ on sulphur nutrition of young pedunculate oak (*Quercus robur* L.) trees. *Plant, Cell and Environment* 19(4):418-426.

Pedunculate oak (*Quercus robur* L.) was germinated and grown at ambient CO₂ concentration and 650 $\mu\text{mol mol}^{-1}$ CO₂ in the presence and absence of the ectomycorrhizal fungus *Laccaria laccata* for a total of 22 weeks under non-limiting nutrient conditions. Sulphate uptake, xylem loading and exudation were analysed in excised roots. Despite a relatively high affinity for sulphate ($K_M = 1.6 \text{ mmol m}^{-3}$), the rates of sulphate uptake by excised lateral roots of mycorrhizal oak trees were low as compared to herbaceous plants. Rates of sulphate uptake were similar in mycorrhizal and non-mycorrhizal roots and were not affected by growth of the trees at elevated CO₂. However, the total uptake of sulphate per plant was enhanced by elevated CO₂ and further enhanced by elevated CO₂ and mycorrhization. Sulphate uptake seemed to be closely correlated with biomass accumulation under the conditions applied. The percentage of the sulphate taken up by mycorrhizal oak roots that was loaded into the xylem was an order of magnitude lower than previously observed for herbaceous plants. The rate of xylem loading was enhanced by mycorrhization and, in roots of mycorrhizal trees only, by growth at elevated CO₂. On a whole-plant basis this increase in xylem loading could only partially be explained by the increased growth of the trees. Elevated CO₂ and mycorrhization appeared to increase greatly the sulphate supply of the shoot at the level of xylem loading. For all treatments, calculated rates of sulphate exudation were significantly lower than the corresponding rates of xylem loading of sulphate. Radiolabelled sulphate loaded into the xylem therefore seems to be readily diluted by unlabelled sulphate during xylem transport. Allocation of reduced sulphur from oak leaves was studied by flap-feeding radiolabelled GSH to mature oak leaves. The rate of export of radioactivity from the fed leaves was 4.5 times higher in mycorrhizal oak trees grown at elevated CO₂ than in those grown at ambient CO₂. Export of radiolabel proceeded almost exclusively in a basipetal direction to the roots. From these experiments it can be concluded that, in mycorrhizal oak trees grown at elevated CO₂, the transport of sulphate to the shoot is increased at the level of xylem loading to enable increased sulphate reduction in the leaves. Increased sulphate reduction seems to be required for the enhanced allocation of reduced sulphur to the roots which is observed in trees grown at elevated CO₂. These changes in sulphate and reduced sulphur allocation may be a prerequisite for the positive effect of elevated CO₂ on growth of oak trees previously observed.

KEYWORDS: CELLS, EFFICIENCY, GROWTH, LONG-DISTANCE TRANSPORT, PLANTS, ROOTS, SEEDLINGS, SULFATE TRANSPORT, SULFUR, TRANSLOCATION

2172

Segal, M., P. Alpert, U. Stein, M. Mandel, and M.J. Mitchell. 1994. Some assessments of the potential 2 X CO₂ climatic effects on water-balance components in the eastern mediterranean. *Climatic Change* 27(4):351-371.

General circulation model (GCM) coarse evaluations of the climatological impact in the Eastern Mediterranean due to global doubling of the atmospheric CO₂ concentration were used as input for a preliminary estimation of modifications in local processes affecting the water balance in this region. It is suggested that: (i) in the 2 x CO₂ climate the average regional change of precipitation associated with typical mid-winter cyclonic systems is relatively small, however, it is associated with redistribution of the regional rainfall; (ii) in the elevated terrain in the northern part of the region, daytime snowmelt due to warm air advection may be enhanced, as much as 2.8 cm per day; and (iii) transpiration in the coastal area of the Eastern Mediterranean may increase by approximately 13% of its current level in the summer and somewhat more in the winter.

KEYWORDS: HEAT-STORAGE, LAYER, MODEL, OCEAN, PRECIPITATION, SENSITIVITY

2173

Seginer, I., C. Gary, and M. Tchamitchian. 1994. Optimal temperature regimes for a greenhouse crop with a carbohydrate pool - a modeling study. *Scientia Horticulturae* 60(1-2):55-80.

A simple crop model with two state variables, namely structural biomass and carbohydrate pool, was used to explore the effect of alternative temperature regimes on greenhouse crop production. Assuming a repeated environmental cycle, certain qualitative predictions could be made. (1) The smaller the plants and the higher the light integral and CO₂ enrichment, the higher are the temperatures which lead to maximum production. (2) Day temperatures higher than night temperatures usually lead to higher production. On winter days, however, an inverse temperature regime may result in energy saving without loss of production. (3) Temperature variations may often be tolerated, provided that the mean temperature (temperature integral) is maintained at the level appropriate for maximum production. A limited amount of published experimental data was used to fit the model, leading to a satisfactory agreement.

KEYWORDS: ENRICHMENT, GROWTH, LEAVES, LEVEL, RESPIRATION, TOMATO PLANTS, TOMGRO, YIELD

2174

Sehmer, L., V. Fontaine, F. Antoni, and P. Dizengremel. 1998. Effects of ozone and elevated atmospheric carbon dioxide on carbohydrate metabolism of spruce needles. Catabolic and detoxification pathways. *Physiologia Plantarum* 102(4):605-611.

We have studied the effects of ozone, carbon dioxide and ozone combined with carbon dioxide fumigations on catabolic and detoxification pathways in spruce (*Picea abies* [L.] Karst.) needles. The results obtained showed an increase in the activities of three enzymes involved in the detoxification pathway, superoxide dismutase (SOD, EC 1.15.1.1), ascorbate peroxidase (AsCPD, EC 1.11.1.11) and glutathione reductase (GR, EC 1.6.4.2) when trees were exposed to ozone and to ozone-carbon dioxide treatments. In these two treatments, the fraction of SOD activity due to the chloroplastic isoform was increased (1.5-fold). In the needles of trees exposed to ozone and to ozone-carbon dioxide fumigation, an increase in the activities of glucose-6-phosphate dehydrogenase (G-6-PDH, EC 1.1.1.49) showed that the cell had the capacity to produce more NADPH necessary for the detoxification. Stimulation of other enzymes of catabolic pathways (fumarase [EC 4.2.1.2], phosphofructokinase [PFK, EC 7.1.1] and

phosphoenolpyruvate carboxylase [PEPC, EC 4.1.1.31]), was also observed making it possible for the cell to provide the reducing power necessary for detoxification as well as energy and carbon skeletons involved in the repair processes. When carbon dioxide alone was applied, no effects could be detected on these enzyme activities. However, when carbon dioxide was combined with ozone, the effect of ozone on trees was less than that induced by ozone alone, suggesting that elevated atmospheric carbon dioxide concentrations may to some extent protect plants from ozone injury.

KEYWORDS: AIR- POLLUTANTS, ASSAY, CO₂, ENZYMES, HYDROGEN- PEROXIDE, NORWAY SPRUCE, PHOSPHOENOLPYRUVATE CARBOXYLASE, PINE, PLANTS, SUPEROXIDE-DISMUTASE

2175

Seko, Y., and M. Nishimura. 1996. Effect of CO₂ and light on survival and growth of rice regenerants grown in vitro on sugar-free medium. *Plant Cell Tissue and Organ Culture* 46(3):257-264.

Rice (*Oryza sativa* L.) plantlets regenerated from callus (rice regenerants) were grown in vitro during the preparation stage either on a 1/4 strength N6 gellan gum (4 g l⁻¹) medium without sucrose (SFM) or with 30 g l⁻¹ sucrose (SCM), and under CO₂ concentrations of 0.4, 2, 10, 50 or 100 mmol mol⁻¹, a photoperiod of 24 h and a photosynthetic photon flux density (PPFD) of 125 μ mol m⁻² s⁻¹. Rice regenerants were also grown in vitro on SFM or SCM under CO₂ concentration of 50 mmol mol⁻¹, a photoperiod of 12 or 24 h and a PPFD of 80 or 125 μ mol m⁻² s⁻¹. All rice regenerants grew successfully on SFM under CO₂ concentrations of 50 or 100 mmol mol⁻¹. Increasing the CO₂ concentration increased the survival percentage, shoot length and shoot and root dry weights of rice regenerants grown on SFM. Increasing CO₂ concentration had no significant effect on the survival or growth of rice regenerants grown on SCM. Survival percentages of rice regenerants grown on SCM were less than 80% for each of the CO₂ concentrations. A photoperiod of 24 h under CO₂ enrichment improved the survival and growth of rice regenerants grown on SFM, and increased the survival percentage and shoot dry weight of rice regenerants grown on SCM.

KEYWORDS: CARBON DIOXIDE, CULTURE, ENRICHMENT, INVITRO, SUCROSE CONCENTRATION

2176

Seligman, N.G., and T.R. Sinclair. 1995. Global environment change and simulated forage quality of wheat .2. Water and nitrogen stress. *Field Crops Research* 40(1):29-37.

Forage crops are frequently subjected to stress conditions resulting from inadequate supplies of water and N. Because forages grown under these stress conditions constitute an important resource in animal agriculture, this study was undertaken to assess possible changes in the nutritive value and productivity of forage crops as a consequence of global environment change. A relatively simple, mechanistic model of wheat was extended to simulate growth and important determinants of feed quality ([N], leaf:stem, dry matter digestibility) in an annual, temperate climate C-3 forage grass. Weather data for a semiarid region and different levels of applied N were used to examine the response of forage productivity to various levels of water and N availability. Not surprisingly, responses to global environment change were highly dependent on the availability of both water and N. When either resource was available at low levels, production of digestible dry matter was nearly unchanged by elevated [CO₂] or increased temperature. When compared at equivalent development stages, small increases in forage quality were simulated, mainly because higher temperature resulted in achievement of the initiation of grain fill at an earlier date. As N

availability increased, differences in forage characteristics and productivity became more prominent. Elevated ambient [CO₂] increased vegetative mass, digestible dry matter, and concentration of digestible dry matter but decreased leaf:stem and [N]. Increased temperature generally had an effect on forage traits that was opposite to the elevated [CO₂] response. The combined effects of both factors sometimes cancelled each other, but usually one of the factors was dominant. Negative effects of temperature tended to be aggravated by dry conditions. At crop maturity, positive effects of elevated atmospheric [CO₂] on forage productivity and quality were severely decreased by nutrient and physiological constraints. These simulations indicate that when forage crops are grown under irrigation in semiarid regions, there may be substantial and complex changes in productivity and feed quality as a consequence of warmer temperature and elevated atmospheric [CO₂]. Under rainfed conditions, these differences could be quite erratic and virtually unpredictable within the current range of interannual variation in forage productivity and quality.

KEYWORDS: CARBOHYDRATE, CARBON DIOXIDE, CO₂-ENRICHMENT, DIGESTIBILITY, DRY-WEIGHT, GROWTH, PLANT, TEMPERATURE, YIELD

2177

Sellers, P.J., F.G. Hall, R.D. Kelly, A. Black, D. Baldocchi, J. Berry, M. Ryan, K.J. Ranson, P.M. Crill, D.P. Lettenmaier, H. Margolis, J. Cihlar, J. Newcomer, D. Fitzjarrald, P.G. Jarvis, S.T. Gower, D. Halliwell, D. Williams, B. Goodison, D.E. Wickland, and F.E. Guertin. 1997. BOREAS in 1997: Experiment overview, scientific results, and future directions. *Journal of Geophysical Research-Atmospheres* 102(D24):28731-28769.

The goal of the Boreal Ecosystem-Atmosphere Study (BOREAS) is to improve our understanding of the interactions between the boreal forest biome and the atmosphere in order to clarify their roles in global change. This overview paper describes the science background and motivations for BOREAS and the experimental design and operations of the BOREAS 1994 and BOREAS 1996 field years. The findings of the 83 papers in this journal special issue are reviewed. In section 7, important scientific results of the project to date are summarized and future research directions are identified.

KEYWORDS: AMAZONIAN FOREST, ATMOSPHERIC CO₂, CANOPY, CARBON DIOXIDE, ENERGY, EXCHANGE, FIELD EXPERIMENT FIVE, GENERAL-CIRCULATION MODEL, LAND-SURFACE, WATER-VAPOR

2178

Sellers, P., F. Hall, H. Margolis, B. Kelly, D. Baldocchi, G. Denhartog, J. Cihlar, M.G. Ryan, B. Goodison, P. Crill, K.J. Ranson, D. Lettenmaier, and D.E. Wickland. 1995. The boreal ecosystem-atmosphere study (boreas) - an overview and early results from the 1994 field year. *Bulletin of the American Meteorological Society* 76(9):1549-1577.

The Boreal Ecosystem Atmosphere Study (BOREAS) is a large-scale international field experiment that has the goal of improving our understanding of the exchanges of radiative energy, heat, water, CO₂, and trace gases between the boreal forest and the lower atmosphere. An important objective of BOREAS is to collect the data needed to improve computer simulation models of the processes controlling these exchanges so that scientists can anticipate the effects of global change. From August 1993 through September 1994, a continuous set of monitoring measurements-meteorology, hydrology, and satellite remote sensing-were gathered over the 1000 x 1000 km BOREAS study region that covers most of Saskatchewan and Manitoba, Canada. This monitoring program was punctuated by six campaigns that saw the

deployment of some 300 scientists and aircrew into the field, supported by 11 research aircraft. The participants were drawn primarily from U.S. and Canadian agencies and universities, although there were also important contributions from France, the United Kingdom, and Russia. The field campaigns lasted for a total of 123 days and saw the compilation of a comprehensive surface-atmosphere flux dataset supported by ecological, trace gas, hydrological, and remote sensing science observations. The surface-atmosphere fluxes of sensible heat, latent heat, CO₂, and momentum were measured using eddy correlation equipment mounted on a surface network of 10 towers complemented by four flux-measurement aircraft. All in all, over 350 airborne missions (remote sensing and eddy correlation) were flown during the 1994 field year. Preliminary analyses of the data indicate that the area-averaged photosynthetic capacity of the boreal forest is much less than that of the temperate forests to the south. This is reflected in very low photosynthetic and carbon drawdown rates, which in turn are associated with low transpiration rates (less than 2 mm day⁻¹ over the growing season for the coniferous species in the area). The strong sensible fluxes generated as a result of this often lead to the development of a deep dry planetary boundary layer over the forest, particularly during the spring and early summer. The effects of frozen soils and the strong physiological control of evapotranspiration in the biome do not seem to be well represented in most operational general circulation models of the atmosphere. Analyses of the data will continue through 1995 and 1996. Some limited revisits to the field are anticipated.

KEYWORDS: CARBON, DYNAMICS, FIFE, MODEL

2179

Seneweera, S.P., A.S. Basra, E.W. Barlow, and J.P. Conroy. 1995. Diurnal regulation of leaf blade elongation in rice by CO₂ - is it related to sucrose-phosphate synthase activity. *Plant Physiology* 108(4):1471-1477.

The relationship between leaf blade elongation rates (LER) and sucrose-phosphate synthase (SPS) activity was investigated at different times during ontogeny of rice (*Oryza sativa* L. cv. Jarrah) grown in flooded soil at either 350 or 700 µmol L⁻¹ CO₂. High CO₂ concentrations increased LER of expanding blades and in vivo activity (V-limiting) SPS activity of expanded blades during the early vegetative stage (21 d after planting [DAP]), when tiller number was small and growing blades were strong carbohydrate sinks. Despite a constant light environment, there was a distinct diurnal pattern in LER, V-limiting SPS activity, and concentration of soluble sugars, with an increase in the early part of the light period and a decrease later in the light period. The strong correlation ($r = 0.65$) between LER and V-limiting SPS activity over the diurnal cycle indicated that SPS activity played an important role in controlling blade growth. The higher V-limiting SPS activity at elevated CO₂ at 21 DAP was caused by an increase in the activation state of the enzyme rather than an increase in V-max. Fructose and glucose accumulated to a greater extent than sucrose at high CO₂ and may have been utilized for synthesis of cell-wall components, contributing to higher specific leaf weight. By the mid-tillering stage (42 DAP), CO₂ enrichment enhanced V-limiting and V-max activities of source blades. Nevertheless, LER was depressed by high CO₂, probably because tillers were stronger carbohydrate sinks than growing blades.

KEYWORDS: CARBON, GROWTH, LEAVES, NITROGEN, PHOTOSYNTHESIS, PLANTS

2180

Seneweera, S., A. Blakeney, P. Milham, A.S. Basra, E.W.R. Barlow, and J. Conroy. 1996. Influence of rising atmospheric CO₂ and phosphorus nutrition on the grain yield and quality of rice (*Oryza sativa* cv. Jarrah). *Cereal Chemistry* 73(2):239-243.

Raising the atmospheric CO₂ concentration from 350 µmol L⁻¹ of CO₂ per liter to a level expected by the end of the next century (700 µmol L⁻¹) influenced both the grain yield and quality of the short-duration rice (*Oryza sativa*) cultivar, Jarrah. Yield was enhanced by up to 58%, primarily due to an increase in grain number, although grain size was also greater at high CO₂. Varying the supply of phosphorus influenced the magnitude of the CO₂ response with greatest responses occurring at medium rather than luxury or low phosphorus supplies. However, yield enhancement by high CO₂ was observed even when phosphorus supply was severely growth limiting. Chemical (amylose and nutrient concentration) and physical (relative paste viscosity) measurements made on the ground grain indicated that cooked rice grain from plants grown under high levels of CO₂ would be firmer. The nutritive value of grain was also changed at high CO₂ due to a reduction in grain nitrogen and, therefore, protein concentration. However, total nitrogen content per grain was unaffected by high CO₂. In contrast, phosphorus content per grain was greater at high CO₂ and there was a strong correlation between magnesium and phosphorus concentrations. These results indicate that there is a need to plan for the inevitable rise in atmospheric CO₂ concentrations by selecting genotypes that will maintain suitable quality characteristics under global change.

KEYWORDS: CARBON DIOXIDE, GROWTH, STARCH

2181

Seneweera, S.P., and J.P. Conroy. 1997. Growth, grain yield and quality of rice (*Oryza sativa* L.) in response to elevated CO₂ and phosphorus nutrition (Reprinted from Plant nutrition for sustainable food production and environment, 1997). *Soil Science and Plant Nutrition* 43:1131-1136.

The influence of rising atmospheric CO₂ concentrations and phosphorus nutrition on growth, grain yield and quality of a early maturing rice cultivar (*Oryza sativa* L. cv. Jarrah) was investigated by growing plants in a range of phosphorus levels at either 350 or 700 µmol L⁻¹ CO₂ in the growth chambers. Total above ground biomass and grain yield were greater at elevated CO₂ concentrations and with increasing phosphorus supply. The CO₂ response was evident at all but the lowest phosphorus treatments but its magnitude was greater at moderate phosphorus supplies. The increase in grain yield at high CO₂ was due mainly to an enhancement of tiller number. The phosphorus concentration in the foliage was unaffected by CO₂ enrichment and the critical concentration of 1.8 g kg⁻¹ dwt was the same as reported for field-grown rice. The concentration of calcium in the foliage was increased by high CO₂ and the nitrogen concentration was reduced. Chemical analysis (amylose and mineral concentration) indicated that cooked rice grain from high-CO₂-grown plants would be firmer and that concentrations of Zn and Fe, which are important in the diet of humans, will be lower. These results indicate that there is a need to plan for the inevitable rise in global CO₂ concentrations by selecting cultivars which will be more productive and yet maintain suitable quality characteristics under elevated CO₂ levels.

KEYWORDS: CARBON DIOXIDE, DURATION, ENRICHMENT, NITROGEN, TEMPERATURE, WHEAT

2182

Seneweera, S.P., O. Ghannoum, and J. Conroy. 1998. High vapour pressure deficit and low soil water availability enhance shoot growth responses of a C-4 grass (*Panicum coloratum* cv. Bambatsi) to CO₂ enrichment. *Australian Journal of Plant Physiology* 25(3):287-292.

The hypothesis that shoot growth responses of C-4 grasses to elevated CO₂ are dependent on shoot water relations was tested using a C-4 grass, *Panicum coloratum* (NAD-ME subtype). Plants were grown for 35 days at CO₂ concentrations of 350 or 1000 µmol L⁻¹. Shoot water relations were altered by growing plants in soil which was brought daily

to 65, 80 or 100% field capacity (FC) and by maintaining the vapour pressure deficit (VPD) at 0.9 or 2.1 kPa. At 350 $\mu\text{mol L}^{-1}$ CO₂, high VPD and lower soil water content depressed shoot dry mass, which declined in parallel at each VPD with decreasing soil water content. The growth depression at high VPD was associated with increased shoot transpiration, whereas at low soil water, leaf water potential was reduced. Elevated CO₂ ameliorated the impact of both stresses by decreasing transpiration rates and raising leaf water potential. Consequently, high CO₂ approximately doubled shoot mass and leaf length at a VPD of 2.1 kPa and soil water contents of 65 and 80% FC but had no effect on unstressed plants. Water use efficiency was enhanced by elevated CO₂ under conditions of stress but this was primarily due to increases in shoot mass. High CO₂ had a greater effect on leaf growth parameters than on stem mass. Elevated CO₂ increased specific leaf area and leaf area ratio, the latter at high VPD only. We conclude that high CO₂ increases shoot growth of C-4 grasses by ameliorating the effects of stress induced by either high VPD or low soil moisture. Since these factors limit growth of field-grown C-4 grasses, it is likely that their biomass will be enhanced by rising atmospheric CO₂ concentrations.

KEYWORDS: ELEVATED CO₂, HUMIDITY

2183

Seneweera, S., P. Milham, and J. Conroy. 1994. Influence of elevated CO₂ and phosphorus-nutrition on the growth and yield of a short-duration rice (*Oryza-sativa* L. CV Jarrah). *Australian Journal of Plant Physiology* 21(3):281-292.

The growth and development of a short-duration rice cultivar (*Oryza sativa* L. cv. Jarrah), grown in flooded soil with a range of phosphorus (P) levels and exposed to atmospheric CO₂ concentrations of either 350 or 700 $\mu\text{mol L}^{-1}$ was followed for 146 days after planting (DAP). Development (estimated by rate of tiller production and time to flowering) was faster with higher soil P levels and CO₂ enrichment, the effect being more pronounced with CO₂ enrichment. During the early vegetative phase (up to 35 DAP), when rates of tiller production were low, shoot growth and rates of leaf expansion were faster at elevated CO₂ concentrations and high soil P levels. Rates of tiller production were greater with these treatments during the 35-56 DAP period, when tillering was at a maximum. Shoot elongation was reduced at elevated CO₂ levels and at high soil P levels during this period. By 146 DAP leaf weight was greater at high P levels, but CO₂ enrichment accelerated tiller production to such an extent that final leaf weight was lower at high CO₂, probably because there were fewer, and smaller, leaves on each tiller. Despite this, grain yield was increased by up to 58% by CO₂ enrichment, with increases occurring even at low soil P levels. This was due mainly to an increase in grain number per panicle, although panicle number also increased. Higher soil P levels also increased grain number and yield. The P concentration in the foliage was unaffected by the CO₂ treatments and the concentration required to produce maximum yield was 0.18% (dry wt basis) at both CO₂ levels. Greater starch accumulation in the stems of high-CO₂-grown plants may have accounted for the higher number of grains in each panicle.

KEYWORDS: ATMOSPHERIC PARTIAL-PRESSURE, CARBON DIOXIDE, NITROGEN, PLANT GROWTH

2184

Senock, R.S., J.M. Ham, T.M. Loughin, B.A. Kimball, D.J. Hunsaker, P.J. Pinter, G.W. Wall, R.L. Garcia, and R.L. LaMorte. 1996. Sap flow in wheat under free-air CO₂ enrichment. *Plant, Cell and Environment* 19(2):147-158.

The effects of elevated carbon dioxide (CO₂) concentration on plant water use are best evaluated on plants grown under field conditions and

with measurement techniques that do not disturb the natural function of the plant. Sap flow gauges were used on individual main stems of wheat (*Triticum aestivum* L. cv Yecora rojo) grown under normal ambient conditions (control) and in a free-air CO₂ enrichment (FACE) system in Arizona with either high (control+high H₂O=CW; FACE+high H₂O=FW) or low (control+low H₂O=CD; FACE+low H₂O=FD) irrigation regimens. Over a 30d period (stem elongation to anthesis), combinations of treatments were monitored with 10-40 gauges per treatment. The effects of increased CO₂ on tiller water use were inconsistent in both the diurnal patterns of sap flow and the statistical analyses of daily sap flow (F-tot). Initial results suggested that the reductions in F-tot from CO₂ enrichment were small (0-10%) in relation to the H₂O treatment effect (20-30%). For a 3d period, F-tot of FW was 19-26% less than that of CW (P=0.10). Examination of the different sources of variation in the study revealed that the location of gauges within the experimental plots influenced the variance of the sap flow measurements. This variation was probably related to positional variation in subsurface drip lines used to irrigate plots. A sampling design was proposed for use of sap flow gauges in FACE systems with subsurface irrigation that takes into account the main treatment effects of CO₂ enrichment and the other sources of variation identified in this study. Despite the small and often statistically non-significant differences in F-tot between the CW and FW treatments, cumulative water use of the FW treatment at the end of the first three test periods ranged from 7 to 23% lower than that of the CW treatment. Differences in sap flow between FW and CW compared well with treatment differences in evapotranspiration. The results of the study, based on the first reported sap flow measurements of wheat, suggest that irrigation requirements for wheat production, in the present climatic regimen of the south-western US, may be predicted to decrease slightly because of increasing atmospheric CO₂.

KEYWORDS: BALANCE, CARBON DIOXIDE, COTTON, GROWTH, RESPONSES, TRANSPIRATION, WATER-USE

2185

Serraj, R., L.H. Allen, and T.R. Sinclair. 1999. Soybean leaf growth and gas exchange response to drought under carbon dioxide enrichment. *Global Change Biology* 5(3):283-291.

This study was conducted to determine the response in leaf growth and gas exchange of soybean (*Glycine max*: Merr.) to the combined effects of water deficits and carbon dioxide (CO₂) enrichment. Plants grown in pots were allowed to develop initially in a glasshouse under ambient CO₂ and well-watered conditions. Four-week old plants were transferred into two different glasshouses with either ambient (360 $\mu\text{mol mol}^{-1}$) or elevated (700 $\mu\text{mol mol}^{-1}$) CO₂. Following a 2-day acclimation period, the soil of the drought-stressed pots was allowed to dry slowly over a 2-week period. The stressed pots were watered daily so that the soil dried at an equivalent rate under the two CO₂ levels. Elevated [CO₂] decreased water loss rate and increased leaf area development and photosynthetic rate under both well-watered and drought-stressed conditions. There was, however, no significant effect of [CO₂] in the response relative to soil water content of normalized leaf gas exchange and leaf area. The drought response based on soil water content for transpiration, leaf area, and photosynthesis provide an effective method for describing the responses of soybean physiological processes to the available soil water, independent of [CO₂].

KEYWORDS: CO₂ EXPOSURE, PHOTOSYNTHESIS, PHYSIOLOGY, RICE, SOIL, STAGE, TEMPERATURE, TRANSPIRATION, WATER-STRESS, WHEAT

2186

Serraj, R., T.R. Sinclair, and L.H. Allen. 1998. Soybean nodulation and N-2 fixation response to drought under carbon dioxide enrichment.

The combined effects of carbon dioxide (CO₂) enrichment and water deficits on nodulation and N-2 fixation were analysed in soybean [*Glycine max* (L.) Merr.]. Two short-term experiments were conducted in greenhouses with plants subjected to soil drying, while exposed to CO₂ atmospheres of either 360 or 700 $\mu\text{mol CO}_2 \text{ mol}^{-1}$. Under drought-stressed conditions, elevated [CO₂] resulted in a delay in the decrease in N₂ fixation rates associated with drying of the soil used in these experiments. The elevated [CO₂] also allowed the plants under drought to sustain significant increases in nodule number and mass relative to those under ambient [CO₂]. The total non-structural carbohydrate (TNC) concentration was lower in the shoots of the plants exposed to drought; however, plants under elevated CO₂ had much higher TNC levels than those under ambient CO₂. For both [CO₂] treatments, drought stress induced a substantial accumulation of TNC in the nodules that paralleled N-2 fixation decline, which indicates that nodule activity under drought may not be carbon limited. Under drought stress, ureide concentration increased in all plant tissues. However, exposure to elevated [CO₂] resulted in substantially less drought-induced ureide accumulation in leaf and petiole tissues. A strong negative correlation was found between ureide accumulation and TNC levels in the leaves. This relationship, together with the large effect of elevated [CO₂] on the decrease of ureide accumulation in the leaves, indicated the importance of ureide breakdown in the response of N-2 fixation to drought and of feedback inhibition by ureides on nodule activity. It is concluded that an important effect of CO₂ enrichment on soybean under drought conditions is an enhancement of photoassimilation, an increased partitioning of carbon to nodules and a decrease of leaf ureide levels, which is associated with sustained nodule growth and N-2 rates under soil water deficits. We suggest that future [CO₂] increases are likely to benefit soybean production by increasing the drought tolerance of N-2 fixation.

KEYWORDS: AMINO-ACID, GAS-EXCHANGE, GROWTH, NITROGENASE ACTIVITY, OXYGEN PERMEABILITY, REDUCTION ACTIVITY, ROOT NODULE ACTIVITY, STRESS, WATER DEFICIT, WHITE CLOVER

2187

Sgherri, C.L.M., M.F. Quartacci, M. Menconi, A. Raschi, and F. Navari-Izzo. 1998. Interactions between drought and elevated CO₂ on alfalfa plants. *Journal of Plant Physiology* 152(1):118-124.

Alfalfa (*Medicago sativa* L.) plants were grown in open top chambers at ambient (340 ppm) and high (600 ppm) CO₂ concentrations. Twenty-five days after the first cutting one set of both plants was subjected to water deficit conditions by withholding water for 5 days. A chamber effect on proteolytic activity, monogalactosyl diacylglycerol to digalactosyl diacylglycerol molar ratio, total non-structural carbohydrates and soluble protein contents occurred. In contrast, no change in leaf water potential was observed between plants grown outdoors and inside the chambers. Plants grown at high CO₂ concentration showed a lower decrease in leaf water potential in comparison with plants grown at atmospheric CO₂ when subjected to water stress. Under high CO₂ concentration leaf nitrogen content decreased whereas starch accumulation and a higher proteolytic activity were recorded. Following water depletion, CO₂-enriched plants showed a decrease in total non- structural carbohydrates and soluble proteins. In thylakoid membranes high CO₂ caused an increase in chlorophyll and lipid contents and a degradation of monogalactosyl diacylglycerol. A higher degree of unsaturation in the main thylakoid lipids was also observed. CO₂-enriched plants were less affected by water stress as shown by reduced chlorophyll degradation and a higher membrane stability.

KEYWORDS: ACIDS, ATMOSPHERIC CARBON-DIOXIDE, FIELD,

2188

Shafer, S.R., U. Blum, S.J. Horton, and D.L. Hesterberg. 1998. Biomass of tomato seedlings exposed to an allelopathic phenolic acid and enriched atmospheric carbon dioxide. *Water, Air, and Soil Pollution* 106(1-2):123-136.

Increased atmospheric CO₂ can affect plant growth, so competition among plants may be influenced. Allelopathy is one mechanism involved in plant competition. Experiments were conducted in a controlled-environment chamber to determine if the concentration of atmospheric CO₂ altered the dose-response relationship between an allelopathic phenolic acid and tomato seedling biomass. Seeds of *Lycopersicon lycopersicum* were planted in quartz sand in styrofoam cups and allowed to germinate and grow for 15-17 days. During the next 14 days, seedlings were watered twice daily with nutrient solution amended with p-coumaric acid (4-hydroxycinnamic acid, HOC₆H₄CH = CHCO₂H; ranging 0-0.85 mg mL⁻¹); 5 concentrations in each experiment) and exposed 24 hr day⁻¹ in continuous-stirred tank reactors (CSTRs) to ambient air (335-375 ppm CO₂) or ambient air to which 350 ppm CO₂ was added (i.e., approximately twice-ambient CO₂; two CSTRs per CO₂ concentration in each experiment). Dose-response data relating p-coumaric acid concentration and shoot, root, and total biomass were fit to a flexible decay function. In all three experiments, twice- ambient CO₂ significantly increased the y-intercept for the dose-response model for the p-coumaric acid effect on shoot biomass by 25-50% but had negligible effects on other aspects of the models. Results suggest that if CO₂ affects plant competition, mechanisms involving allelopathic phenolic acids may not be involved.

KEYWORDS: ANNUALS, CO₂- ENRICHMENT, CUCUMBER LEAF EXPANSION, ELEVATED CO₂, FERULIC ACID, GROWTH, INHIBITION, NUTRIENT CULTURE, PLANT-RESPONSES, RESOURCE USE

2189

Shainisky, L.J., and S.R. Radosevich. 1992. Mechanisms of competition between douglas-fir and red alder seedlings. *Ecology* 73(1):30-45.

Mechanisms of interactions between Douglas-fir (*Pseudotsuga menziesii*) and red alder (*Alnus rubra*) seedlings were assessed in experimentally manipulated stands. The density of each species was varied systematically, creating a matrix of competitive regimes that consisted of five monoculture densities and 25 mixtures of all possible pairwise combinations of the monoculture densities. Response surfaces for growth rates, leaf area, photon flux density, soil moisture content and depletion, and plant water potential were generated within the matrix. Regression coefficients quantified the effects of species densities on response variables, and correlation analysis yielded insight into interrelationships between variables. Tree performance, leaf area per square metre of ground surface area, resources, and physiological variables were all quantitatively altered by alder density, Douglas-fir density, and the interaction between species densities. Alder was the dominant competitor and overtopped the Douglas-fir. Competition for light was mediated by density effects on the leaf area of each species per square metre of ground surface area. Increasing alder leaf area reduced the light reaching the understory Douglas-fir. In contrast, increasing Douglas-fir leaf areas increased the light penetrating through to the understory conifers, due to Douglas-fir's suppression of alder leaf area per square metre. Soil moisture limitations were also created by increasing the density of both species and resulted in increasingly negative leaf water potentials for both species. Growth rates concurrently declined as plant water stress increased. Response variables were assembled into a conceptual modeling proposing how species density

regulated growth through the interactions between resource limitations and impairment of physiological function.

KEYWORDS: CANOPY LEAF-AREA, CARBON RELATIONS, CENTRAL EUROPEAN HEDGEROW, ELEVATED CO₂, GROWTH, INTERFERENCE, PLANTATIONS, PLANTS, PRODUCTIVITY, WATER RELATIONS

2190

Sharma, A., and U.K. Sengupta. 1997. Carbon allocation and partitioning in *Vigna radiata* (L.) Wilczek as affected by additional carbon gain. *Photosynthetica* 34(3):419-426.

Carbon allocation to the source leaf export and partitioning to the sink were studied in mungbean supplied by additional carbon from the source leaves subjected to high CO₂ concentrations (600 and 900 cm³ m⁻³) in three metabolic and functional source-sink combinations. The plants were pruned to a source-path-sink system. With CO₂ enrichment there was an appreciable increase in net photosynthetic CO₂ uptake in earlier formed and physiologically younger leaves. Most of the carbon fixed as a result of enrichment was translocated out of the source leaf within one diurnal cycle. The carbon remaining in the source leaf was unchanged. Partitioning of extra carbon into starch or sugar depended upon the amount of extra carbon synthesized. The unloading of the extra carbon into sinks depended on whether it was used for growth or stored. Under increased carbon content, the leaf as a sink was able to reorganize its metabolic reactions more rapidly to maintain the required gradient for unloading than the pod acting as the sink.

KEYWORDS: CO₂ EXCHANGE, DIOXIDE ENRICHMENT, LEAF, LEAVES, METABOLISM, PHOTOSYNTHESIS, RATES, TRANSLOCATION

2191

Sharma-Natu, P., F.A. Khan, and M.C. Ghildiyal. 1997. Photosynthetic acclimation to elevated CO₂ in wheat cultivars. *Photosynthetica* 34(4):537-543.

Wheat (*T. aestivum*) cvs. Kalyansona and Kundan grown under atmospheric (CA) and elevated CO₂ concentrations (650-150 cm³ m⁻³) - CE) in open top chambers were examined for net photosynthetic rate (P-N), stomatal limitation (I(S)) of P-N, ribulose-1,5-bisphosphate carboxylase (RuBPC) activity, and saccharide content of the leaves. The P-N values of both CA- and CE-grown plants compared at the same CO₂ concentration showed a down regulation under CE at the post-anthesis stage. The negative acclimation of P-N appeared to be due to both stomatal and mesophyll components, and the RuBPC activity got also adjusted. There was a decrease in activation state of RuBPC under CE. In connection with this, an increased accumulation of saccharides in wheat leaf under CE was observed. Kalyansona, owing to its larger sink potential in terms of the number of grains, showed a greater enhancement under CE in both post-ear emergence dry matter production and grain yield. Under CE, this cultivar also showed a lower down regulation of P-N than Kundan.

KEYWORDS: ATMOSPHERIC CO₂, CARBON DIOXIDE, CARBOXYLASE ACTIVITY, DIURNAL CHANGES, ENHANCED CO₂, EXCHANGE, GROWTH, LEAVES, LONG-TERM, PLANTS

2192

Shaver, G.R., W.D. Billings, F.S. Chapin, A.E. Giblin, K.J. Nadelhoffer, W.C. Oechel, and E.B. Rastetter. 1992. Global change and the carbon balance of arctic ecosystems. *BioScience* 42(6):433-441.

KEYWORDS: ACCUMULATION, ALASKAN TUSsock TUNDRA,

BOREAL FORESTS, CLIMATE, CO₂, DIOXIDE, ERIOPHORUM VAGINATUM, GROWTH, NITROGEN, NUTRIENT

2193

Sheehy, J.E., F. Gastal, P.L. Mitchell, J.L. Durand, G. Lemaire, and F.I. Woodward. 1996. A nitrogen-led model of grass growth. *Annals of Botany* 77(2):165-177.

This model is built by considering the utilization rate of nitrogen as the first step in calculating the rate of growth of the various organs of a grass crop. The amount of carbohydrate determines whether there are sufficient carbon skeletons and sufficient energy available to support synthesis of new material. Growth of roots, tillers/stems and leaves is simulated with leaf divided into photosynthetic and non-photosynthetic structures. The model keeps account of soluble carbohydrate and nitrogen pools in each of the organs and storage pools of carbohydrate in the leaves and roots. The modelled crop has an age structure so that each plant organ has an age profile describing daily changes in growth; when the oldest tissue becomes senescent a fraction of its nitrogen is recycled. Seasonal changes in the percentage nitrogen content of the crop, when large amounts of soil nitrogen are available, are shown to be a consequence of changes in both soluble and stored carbohydrate. The contrast between high and low nitrogen treatments is shown to be a consequence of different allocation priorities for nitrogen. The model demonstrates that considering nitrogen as the primary element of synthesis provides an approach that predicts dry matter production successfully, as well as giving a different perspective of the growth processes, and suggesting that the capacity of the enzymatic processes governing synthesis ultimately limits crop yields. This different perspective may be most useful when trying to understand what controls growth and the relative influence of environmental changes on the physiology and morphology of the crop. (C) 1996 Annals of Botany Company

KEYWORDS: CO₂-ENRICHMENT, CROPS, ECOSYSTEMS, ELEVATED CARBON-DIOXIDE, LEAF, LOLIUM-PERENNE, PERENNIAL RYEGRASS, PLANT GROWTH, RESPONSES

2194

Sheppard, M.I., L.L. Ewing, and J.L. Hawkins. 1994. Soil processes and chemical-transport - soil degassing of C-14 dioxide - rates and factors. *Journal of Environmental Quality* 23(3):461-468.

Soil air normally contains elevated levels of CO₂ relative to the atmosphere. The primary source of soil C is plant-root and microbial respiration. The exchange of soil and atmospheric CO₂ is important to many environmental concerns, such as acid rain, global warming and waste management. Proposed disposal of high-level nuclear wastes containing primarily inorganic C-14 may provide a source of (CO₂)-C-14 to the atmosphere. Field and laboratory experiments show that (CO₂)-C-14 Soil degassing rate constants, the flux density (Bq.M².s⁻¹) divided by soil inventory (Bq-m⁻²), range from -10(-7) to -10(-2) S⁻¹, and that the loss of inorganic C-14 is driven primarily by gaseous diffusion. These constants are affected by soil pH and porosity, with smaller influences of soil temperature, moisture and organic matter content. Degassing rate constants derived through mass balance calculations to estimate loss differ only by 20% from direct trapping methods. Frozen soil degassing rate constants were up to 25 times smaller than lab values, indicating that annual C-14 loss rates in northern climates would be lower because of reduced gaseous diffusion during the winter months. Using our field data, we recommend an annual C-14 soil degassing rate constant of -1 x 10(-6) s⁻¹ for acidic soils and a value of -5 x 10(-7) S⁻¹ for calcareous soils. For probabilistic assessment modelling, we recommend a geometric mean degassing constant of -4.3 x 10(-7) S⁻¹ with a geometric standard deviation of 3.26 for three different soils. This indicates the median half-life of C-14

in surface soils is 18 d, with a 99% confidence interval of 13 h and 640 d.

KEYWORDS: CO₂, GAS-TRANSPORT, LAW, MODEL, NUCLEAR-FUEL WASTE, UNSATURATED ZONE, VADOSE ZONE

2195

Sheu, B.H., and C.K. Lin. 1999. Photosynthetic response of seedlings of the sub-tropical tree *Schima superba* with exposure to elevated carbon dioxide and temperature. *Environmental and Experimental Botany* 41(1):57-65.

Seedlings of *Schima superba* were exposed to both ambient (375 ppm) and 720 ppm levels of CO₂ in combination with two incubation temperatures (25/20, 30/25 degrees C, day/night) for a six-month period. Net height growth of seedlings was enhanced in the early period of exposure to high levels of CO₂. However, when seedlings were exposed for a longer period of time to this high concentration, net height growth was inhibited. Decreased photosynthetic rate with elevated CO₂ was observed when measured in the ambient CO₂ over a long-term exposure of 6 months. In contrast, a significant increase in photosynthesis was noted for seedlings exposed to higher incubation temperature in either ambient or 720 ppm CO₂ concentrations. The response of CO₂ assimilation to internal C_i was indicated by the lower sensitivity in seedlings grown in elevated CO₂ concentration. Though this response could also be found in a higher sensitivity in seedlings grown at higher temperature, the seedlings grown in normal conditions (ambient CO₂ and temperature) were still more sensitive to CO₂ assimilation response to internal C_i. This experiment suggests that: (1) exposure of seedlings to higher CO₂ levels for longer periods may lead to a decrease in seedling height growth and photosynthetic rate, as well as decreasing sensitivity to changing internal CO₂ concentrations; (2) the optimum temperature for photosynthesis of seedlings grown in an elevated CO₂ concentration was higher than that for seedlings grown in ambient concentration. (C) 1999 Elsevier Science B.V. All rights reserved.

KEYWORDS: ACCLIMATION, ALLOCATION, CARBOXYLASE, GROWTH, HIGH ATMOSPHERIC CO₂, PERSPECTIVE, PLANTS, PRODUCTIVITY, SOURCE-SINK RELATIONS

2196

Shipley, B., M. Lechowicz, S. Dumont, and W.H. Hendershot. 1992. Interacting effects of nutrients, pH-al and elevated co₂ on the growth of red spruce (*picea-rubens sarg*) seedlings. *Water, Air, and Soil Pollution* 64(3-4):585-600.

A 4 mo growth chamber experiment was conducted to evaluate the presence and importance of interactions between nutrient supply, atmospheric CO₂ concentration, and four different combinations of pH - Al concentration on the growth, vitality, and tissue element concentrations of 1-yr-old red spruce seedlings. Solution chemistry was chosen to simulate soil conditions at a red spruce die-back site at Roundtop Mountain (Quebec) that has high acid loadings. CO₂ levels were chosen to simulate ambient levels and those expected in the next century. All three experimental factors affected growth and all factors except CO₂ affected the visual symptoms of die-back. There was an important interaction between nutrient levels and the different pH - Al combinations, indicating that the response of red spruce to various pH and Al concentrations changes with soil fertility. The positive growth response to enriched CO₂ was not sufficient to offset the negative effects of the acid rain induced stresses. A principal component analysis showed that multivariate functions of foliar element concentrations could clearly distinguish plants from different experimental regimes.

KEYWORDS: ACID-RAIN, ALUMINUM, CARBON DIOXIDE, CLIMATE, FORESTS, INCREASING CO₂, LOBLOLLY-PINE, OZONE,

RESPONSES, TREE SEEDLINGS

2197

Shugart, H.H., T.M. Smith, and W.M. Post. 1992. The potential for application of individual-based simulation- models for assessing the effects of global change. *Annual Review of Ecology and Systematics* 23:15-38.

KEYWORDS: BOREAL FORESTS, CO₂-INDUCED CLIMATE CHANGE, COMPUTER-MODEL, ENVIRONMENTAL-FACTORS, EVALUATING PERFORMANCE, FOREST SUCCESSION MODELS, INTERIOR ALASKA, PLANT- COMMUNITIES, STAND DEVELOPMENT, VEGETATION DYNAMICS

2198

Sicher, R. 1995. Diurnal amylolytic activity in soybean leaves grown at ambient and elevated co₂. *Plant Physiology* 108(2):55.

2199

Sicher, R.C. 1997. Irradiance and spectral quality affect chlorosis of barley primary leaves during growth in elevated carbon dioxide. *International Journal of Plant Science* 158(5):602-607.

The development of chlorosis was studied in primary leaves of barley plants (*Hordeum vulgare* L. cv. Brant) grown at ambient and twice-ambient CO₂ partial pressures. Leaf yellowing was observed 17 d after sowing when plants were grown in controlled environment chambers equipped with high-intensity discharge lamps at an irradiance of 800 μ mol quanta m⁻² s⁻¹. The extent of leaf yellowing, measured as changes of total chlorophyll, increased when the CO₂ partial pressure was raised from 37 to 70 Pa. Chlorosis was increased further by increasing the irradiance from 800 to 1100 μ mol quanta m⁻² s⁻¹. Rates of photosynthetic O₂ evolution by primary leaves, measured 17 d after sowing, were 20% lower for elevated compared with ambient CO₂-grown plants. This result agreed with the level of chlorosis. However soluble protein, Rubisco protein (ribulose, 1,5-bisphosphate carboxylase/oxygenase), and initial and total Rubisco activity 17 d after sowing were unaffected by CO₂ enrichment and the extent of chlorosis. Leaf starch, sucrose, and glucose were increased by elevated CO₂ treatment at almost every sampling. However, only glucose was correlated with leaf damage. Leaf yellowing also was observed on primary leaves of plants grown under microwave-powered sulfur lamps at 800 but not at 550 μ mol quanta m⁻² s⁻¹. The extent of leaf yellowing on plants grown under microwave- powered sulfur lamps was unaffected by CO₂ enrichment. It was concluded that leaf yellowing was influenced by irradiance, photoquality, and CO₂ enrichment. Photobleaching of antenna chlorophyll, rather than premature senescence, was the most likely cause of visible leaf injury in barley.

KEYWORDS: ACCUMULATION, CARBOHYDRATE, CHLOROPHYLL CONTENT, CO₂ CONCENTRATION, ENRICHMENT, FOLIAR DEFORMATION, FRUIT PRODUCTION, HIGH-PRESSURE SODIUM, PLANTS, TOMATO GENOTYPES

2200

Sicher, R.C. 1998. Yellowing and photosynthetic decline of barley primary leaves in response to atmospheric CO₂ enrichment. *Physiologia Plantarum* 103(2):193-200.

The photosynthetic response of barley (*Hordeum vulgare* L. cv. Brant) primary leaves was studied as a function of chlorosis induced by CO₂ enrichment. Leaf yellowing; measured as changes of chlorophyll a and b, was more extensive in controlled environments at elevated (680 \pm 17

mu l l(-1)) than at ambient (380 +/- 21 mu l l(-1)) CO₂. Stomatal conductance of primary leaves was decreased by growth in elevated CO₂ between 11 and 18 days after sowing (DAS) when measured at both 380 and 680 mu l l(-1) CO₂. Internal leaf CO₂ concentration (C-i) was also lower for elevated- compared to ambient-CO₂-grown primary leaves between 11 and 14 DAS. Results suggest that non-stomatal factors were responsible for the decreased photosynthetic rates of elevated- compared to ambient-CO₂-grown primary leaves 18 DAS. Various photochemical measurements, including quantum absorptance (alpha), minimal (F-0), maximal (F-m), and variable (F-v) chlorophyll fluorescence, as well as the F-v/F-m ratio, were significantly decreased 18 DAS in the elevated- compared to ambient-CO₂ treatment. Photochemical (q(P)) and nonphotochemical (q(N)) chlorophyll fluorescence quenching: coefficients of 18-day-old primary leaves did not differ between CO₂ treatments. Photosynthetic electron transport rates of photosystem II were slightly lower for elevated- compared to ambient-CO₂-grown primary leaves 18 DAS. Concentrations of alpha-amino N (i.e. free amino acids) in barley primary leaves were increased by CO₂ enrichment 10 DAS, but subsequently, alpha-amino N decreased in association with photosynthetic decline. Total acid protease activity was greater in elevated- than in ambient-CO₂-grown leaves 18 DAS. The above findings suggest that photoinhibition and premature senescence were factors in the CO₂-dependent yellowing of barley primary leaves.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, CHLOROPHYLL FLUORESCENCE, FOLIAR DEFORMATION, FRUIT PRODUCTION, GROWTH, LEAF, LONG-TERM EXPOSURE, TOMATO, WHEAT, YIELD

2201

Sicher, R.C. 1999. Photosystem-II activity is decreased by yellowing of barley primary leaves during growth in elevated carbon dioxide. *International Journal of Plant Science* 160(5):849-854.

Leaf yellowing was studied in 10-18-d-old barley seedlings (*Hordeum vulgare* L. cv. Brant) grown at ambient (38 Pa) and at elevated (68, 100, and 140 Pa) CO₂ partial pressures in controlled-environment chambers. Maximal total chlorophyll (Chl) concentrations of primary leaves from all four CO₂ growth treatments were 0.36 +/- 0.01 g m(-2), and these concentrations were observed 10-12 d after sowing (DAS). Total Chl levels in primary leaves were 35%, 64%, and 78% below maximal levels in the 38, 68, and 100 Pa CO₂ growth treatments, respectively, when measured 18 DAS. Losses of Chl in 18-d-old primary leaves were similar in the 100 and 140 Pa CO₂ treatments. Decreases of Chl a and Chl b in response to CO₂ enrichment were comparable in isolated chloroplast preparations and in intact 18-d-old barley primary leaves of plants grown at 38 and 68 Pa CO₂. Total thylakoid membrane proteins, the Chl a/b binding protein (LHC-II), and D1 protein levels were also lower in chloroplast preparations from plants grown in the elevated compared to the ambient CO₂ treatment. Both ferricyanide reduction and whole-chain electron-transport rates (H₂O --> methylviologen) were significantly lower for chloroplasts from plants grown at 68 Pa CO₂ compared with those grown at 38 Pa CO₂. However, photosystem-I-dependent chloroplast photoreductions did not differ between CO₂ treatments. The results indicated that the CO₂-dependent yellowing of barley primary leaves adversely affected photosystem-II activity. Growth in elevated CO₂ may have increased the susceptibility of photosystem-II to light damage.

KEYWORDS: ATMOSPHERIC CO₂ ENRICHMENT, CHLOROPHYLL, CHLOROSIS, EXCHANGE, FOLIAR DEFORMATION, IRRADIANCE, PHOTOSYNTHESIS, PLANTS, PROTEINS, TOMATO

2202

Sicher, R.C., and J.A. Bunce. 1997. Relationship of photosynthetic acclimation to changes of Rubisco activity in field-grown winter wheat

and barley during growth in elevated carbon dioxide. *Photosynthesis Research* 52(1):27-38.

The responses of photosynthesis, Rubisco activity, Rubisco protein, leaf carbohydrates and total soluble protein to three carbon dioxide treatments were studied in winter wheat [*Triticum aestivum* (L.)] and barley [*Hordeum vulgare* (L.)]. Barley and wheat plants were grown in small field plots during 1995 and 1996 in clear, acrylic chambers (1.2-2.4 m(2)) and were provided with continuous carbon dioxide fertilization at concentrations of 350, 525 and 700 mu mol mol(-1). Photosynthetic rates of barley penultimate leaves and wheat flag leaves measured at growth carbon dioxide concentrations decreased with leaf age in all three CO₂ treatments during 1995 and 1996. Photosynthetic acclimation to elevated CO₂ was observed on seven of eight measurement dates for barley and ten of eleven measurement dates for wheat over both years. Initial Rubisco activity, total soluble protein and Rubisco protein in barley penultimate leaves and wheat flag leaves also decreased with leaf age. Total Rubisco activity was not used because of enzyme degradation. There was a significant CO₂ treatment effect on initial Rubisco activity, total soluble protein and Rubisco protein for wheat in 1995 and 1996 and for barley in 1995. Responses of barley penultimate leaf Rubisco activity and leaf protein concentrations to elevated carbon dioxide were nonsignificant in 1996. A significant CO₂ treatment effect also was detected when means of Rubisco activity, soluble protein and Rubisco protein for wheat flag leaves were combined over harvests and years. These three flag leaf parameters were not significantly different in the 350 and 525 mu mol mol(-1) CO₂ treatments but were decreased during growth in 700 mu mol mol(-1) CO₂ relative to the other two CO₂ treatments. Ratios of photosynthesis at 700 and 350 mu mol mol(-1) were compared to ratios of Rubisco activity at 700 and 350 mu mol mol(-1) using wheat flag leaf data from 1995 and 1996. Regression analysis of these data were linear [$y = 0.586 + 1.103x(r^2 = 0.432)$] and were significant at P less than or equal to 0.05. This result indicated that photosynthetic acclimation was positively correlated with changes of initial Rubisco activity in wheat flag leaves in response to CO₂ enrichment. Effects of elevated CO₂ on wheat leaf proteins during 1995 and 1996 and on barley during 1995 were consistent with an acceleration of senescence.

KEYWORDS: ATMOSPHERIC CO₂, ENRICHMENT, PLANTS, PROTEINS, RIBULOSE-1,5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, YIELD

2203

Sicher, R.C., and J.A. Bunce. 1998. Evidence that premature senescence affects photosynthetic decline of wheat flag leaves during growth in elevated carbon dioxide. *International Journal of Plant Science* 159(5):798-804.

Net CO₂ exchange (NCE) rates and various flag leaf constituents were measured in wheat plants (*Triticum aestivum* L.) grown in field chambers at either 350 or 700 mu l l(-1) CO₂. Rates of NCE decreased with leaf age in both CO₂ treatments during 1997. A stimulation of NCE initially occurred in response to CO₂ enrichment, but this was not observed on the final eight of 33 experimental days. Net photosynthetic rates in response to growth at elevated CO₂ were decreased ca. 22% on average for all measurement dates in 1997 and when all NCE rates measured at elevated CO₂ for 1995-1997 were averaged (P less than or equal to 0.0001). Soluble protein, alpha-amino nitrogen, and Chl a + b concentrations were significantly lower (P less than or equal to 0.0001) in elevated compared with ambient CO₂-grown wheat flag leaves in 1997. The treatment by date interactions for these flag leaf constituents were nonsignificant (P greater than or equal to 0.05). Flag leaf storage carbohydrates were measured on 10 dates in 1997, but only starch and sucrose were affected by the elevated CO₂ treatment. An increase of acid proteinase activity was observed on the last two measurement dates of this study. However, changes of acid proteinase activity were unaffected

by CO₂ enrichment (P greater than or equal to 0.05) and only occurred during late stages of senescence. These findings supported the suggestion that premature senescence contributed to the photosynthetic decline observed in wheat flag leaves during growth at elevated CO₂. Changes of alpha-amino nitrogen were correlated with photosynthetic decline, but acid proteinase activity probably was under endogenous control.

KEYWORDS: ACCLIMATION, ACCUMULATION, CARBOXYLASE, ENRICHMENT, GRAIN-GROWTH, INCREASING ATMOSPHERIC CO₂, LEAF, NITROGEN REDISTRIBUTION, PROTEINS, TRITICUM-AESTIVUM L

2204

Sicher, R.C., and D.F. Kremer. 1994. Responses of nicotiana-tabacum to co₂ enrichment at low-photon flux-density. *Physiologia Plantarum* 92(3):383-388.

Effects of CO₂ enrichment on photosynthesis and on dry matter allocation were examined in two tobacco (*Nicotiana tabacum* L.) genotypes, Samsun and W38. Plants were grown from seed in controlled environment chambers at a photosynthetic photon flux density of 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Averaged over the 9 day study, net photosynthesis rates were 14.2 \pm 0.5 and 13.0 \pm 0.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in elevated (70 Pa) and in ambient (35 Pa) CO₂ air, respectively, when measured at the irradiance and CO₂ partial pressure employed for plant growth. However, photosynthesis rates of plants grown in elevated CO₂ were 50% less than those of the ambient controls on the last day of treatment, when measured at 70 Pa CO₂ air and an irradiance of 900 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Total plant dry weight and specific leaf weight were greater (P<0.05) in enriched-CO₂-grown than in ambient-CO₂-grown plants. Leaf starch, measured during the first hour of the photoperiod, increased over 7 days of treatment in elevated-CO₂-grown but not in ambient-CO₂-grown plants. Ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) activities of tobacco plants grown at 35 and 70 Pa CO₂ air were 58.5 \pm 4.5 and 48.5 \pm 3.7 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively, between days 0 and 9 of the study. Rubisco activation state, Rubisco protein concentration, soluble protein and total chlorophyll were unaffected by CO₂ enrichment. The above findings demonstrated that photosynthesis was down regulated in tobacco plants after 7 to 9 days of CO₂ enrichment at low photosynthetic photon flux density, but less than at moderate irradiances.

KEYWORDS: ACCLIMATION, ANTISENSE RBCS, CARBON-DIOXIDE CONCENTRATION, ELEVATED CO₂, GROWTH, HIGH ATMOSPHERIC CO₂, LEAVES, PHOTOSYNTHESIS, RIBULOSE BISPHOSPHATE CARBOXYLASE, RIBULOSE-1,5-BISPHOSPHATE CARBOXYLASE-OXYGENASE

2205

Sicher, R.C., and D.F. Kremer. 1996. Rubisco activity is altered in a starchless mutant of *Nicotiana sylvestris* grown in elevated carbon dioxide. *Environmental and Experimental Botany* 36(4):385-391.

Dry matter and net photosynthesis of a wild type and a starchless mutant NS 458 of *Nicotiana sylvestris* (Speg. et Comes) were studied after 25 d of CO₂ enrichment. Plants were grown from seed in controlled environment chambers and treatments of either ambient (35 Pa) or twice ambient (70 Pa) CO₂ were initiated when plants were 3-4 weeks old. Photosynthetic rates measured at 35 and 70 Pa CO₂ and at 900 $\mu\text{mol m}^{-2} \text{s}^{-1}$ were unaffected (P>0.05) by 25 d of CO₂ enrichment. However, a CO₂-by-genotype interaction was observed indicating that photosynthetic rates of the wild type but not the mutant at 35 Pa CO₂ differed in response to CO₂ enrichment. Photosynthetic enhancement was greater (P < 0.001) in the wild type than in the mutant when the measurement CO₂ was doubled. Total biomass and leaf areas of the

mutant and wild type also were unaffected by CO₂ enrichment, although specific leaf weight increased 27% and 13% (P<0.001) for the wild type and mutant lines, respectively. Neither chlorophyll nor soluble leaf protein were affected by CO₂ enrichment. Starch, sucrose, glucose and fructose in wild type and mutant leaf samples were also unaffected by CO₂ enrichment. Rubisco protein levels of the wild type and mutant were about 20% lower in elevated compared to ambient CO₂-grown plants. Initial and total Rubisco activities of wild type and mutant leaf samples were not significantly different (P>0.05) between CO₂ environments. However, initial Rubisco activity was more than 30% lower in mutant than in wild type samples when results from ambient and elevated CO₂-grown plants were combined. Ribulose 1,5-bisphosphate and 3-phosphoglycerate were 280% and 28% greater in the mutant than in the wild type, respectively. These findings suggested that photosynthesis rates of the mutant were limited by Rubisco activity at 35 Pa CO₂ and that end product synthesis rates limited photosynthesis of the mutant at 70 Pa CO₂.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO₂, C-3 PLANTS, CARBOXYLASE, ENZYME, LEAVES, PHOSPHOGLUCOMUTASE, PHOTOSYNTHESIS, STEADY-STATE

2206

Sicher, R.C., D.F. Kremer, and J.A. Bunce. 1995. Photosynthetic acclimation and photosynthate partitioning in soybean leaves in response to carbon dioxide enrichment. *Photosynthesis Research* 46(3):409-417.

Photosynthetic rates and photosynthate partitioning were studied in three-week-old soybean [*Glycine max* (L.) Merr. cv. Williams] plants exposed to either ambient (35 Pa) or elevated (70 Pa) CO₂ in controlled environment chambers. Ambient CO₂-grown plants also were given a single 24 h treatment with 70 Pa CO₂ 1 d prior to sampling. Photosynthetic rates of ambient CO₂-grown plants initially increased 36% when the measurement CO₂ was doubled from 35 to 70 Pa. Photosynthetic rates of the third trifoliolate leaf, both after 1 and 21 d of elevated CO₂ treatment, were 30 to 45% below those of ambient CO₂-grown plants when measured at 35 Pa CO₂. These reduced photosynthetic rates were not due to increased stomatal resistance and were observed for 2 to 8 h after plants given 1 d of CO₂ enrichment were returned to ambient CO₂. Initial and total ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) activities, percent activation, Rubisco protein, soluble protein and leaf chlorophyll content were similar in all CO₂ treatments. Quantum yields of photosynthesis, determined at limiting irradiances and at 35 Pa CO₂, were 0.049 \pm 0.003 and 0.038 \pm 0.005 mol CO₂ fixed per mol quanta for ambient and elevated CO₂-grown plants, respectively (p < 0.05). Leaf starch and sucrose levels were greater in plants grown at 70 than at 35 Pa CO₂. Starch accumulation rates during the day were greater in ambient CO₂-grown plants than in plants exposed to elevated CO₂ for either 1 or 21 d. However, the percentage of C partitioned to starch relative to total C fixed was unaffected by 1 d of CO₂ enrichment. The above results showed that both photosynthetic and starch accumulation rates of soybean leaflets measured at 35 Pa CO₂ were temporarily reduced after 1 and 21 d of CO₂ enrichment. The biochemical mechanism affecting these responses was not identified.

KEYWORDS: CARBOHYDRATE, ELEVATED ATMOSPHERIC CO₂, EXPOSURE, GROWTH, LIGHT, RIBULOSE BISPHOSPHATE CARBOXYLASE, SEEDLINGS, STARCH, SUCROSE SYNTHESIS, TEMPERATURE

2207

Sicher, R.C., D.F. Kremer, and S.R. Rodermel. 1993. Role of rubisco during acclimation of transformed tobacco to co₂ enriched atmospheres. *Plant Physiology* 102(1):88.

2208

Sicher, R.C., D.F. Kremer, and S.R. Rodermel. 1994. Photosynthetic acclimation to elevated CO₂ occurs in transformed tobacco with decreased ribulose-1,5-bisphosphate carboxylase/oxygenase content. *Plant Physiology* 104(2):409-415.

Inhibition of net carbon assimilation rates during growth at elevated CO₂ was studied in transgenic tobacco (*Nicotiana tabacum* L.) plants containing zero to two copies of antisense DNA sequences to the small subunit polypeptide (rbcS) gene of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco). High- and low-Rubisco tobacco plants were obtained from the selfed progeny of the original line 3 transformant (S.R. Rodermel, M.S. Abbott, L. Bogorad [1988] *Cell* 55: 673-681). Assimilation rates of high- and low-Rubisco tobacco plants increased 22 and 71%, respectively, when transferred from 35- to 70-Pa CO₂ chamber air at 900 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photon flux density. However, CO₂-dependent increases of net carbon assimilation rates of high- and low-Rubisco plants virtually disappeared after 9 d of growth in elevated CO₂ chamber air. Total above-ground dry matter production of high- and low-Rubisco plants was 28 and 53% greater, respectively, after 9 d of growth at 70 Pa compared with 35 Pa CO₂. Most of this dry weight gain was due to increased specific leaf weight. Rubisco activity, Rubisco protein, and total chlorophyll were lower in both high- and low-Rubisco plants grown in enriched compared with ambient CO₂ chamber air. Soluble leaf protein also decreased in response to CO₂ enrichment in high- but not in low-Rubisco tobacco plants. Decreased Rubisco activities in CO₂-adapted high- and low-Rubisco plants were not attributable to changes in activation state of the enzyme. Carbonic anhydrase activities and subunit levels measured with specific antibodies were similar in high- and low-Rubisco tobacco plants and were unchanged by CO₂ enrichment. Collectively, these findings suggested that photosynthetic acclimation to enriched CO₂ occurred in tobacco plants either with or without transgenically decreased Rubisco levels and also indicated that the down-regulation of Rubisco in CO₂-adapted tobacco plants was related to decreased specific activity of this enzyme.

KEYWORDS: ANHYDRASE, ANTISENSE RBES, CARBON DIOXIDE, GROWTH, HIGH ATMOSPHERIC CO₂, LIGHT, OXYGENASE, PLANTS, PROTEIN, RIBULOSE BISPHOSPHATE CARBOXYLASE

2209

Siebbe, K., and E. Weis. 1995. Imaging of chlorophyll-a-fluorescence in leaves: Topography of photosynthetic oscillations in leaves of *Glechoma hederacea*. *Photosynthesis Research* 45(3):225-237.

Images of chlorophyll-alpha-fluorescence oscillations were recorded using a camera-based fluorescence imaging system. Oscillations with frequencies around 1 per min were initiated by a transient decrease in light intensity during assimilation at an elevated CO₂-concentration. The oscillation was inhomogeneously distributed over the leaf. In cells adjacent to minor veins, frequency and damping rate was high, if there was any oscillation. In contrast, the amplitude was highest in cells most distant from phloem elements (maximal distance about 300 μm). The appearance of minor veins in oscillation images is explained by a gradient in the metabolic control in the mesophyll between minor veins and by transport of sugar from distant cells to phloem elements. The potential of fluorescence imaging to visualize 'microscopic' source-sink interactions and metabolic domains in the mesophyll is discussed.

KEYWORDS: CALVIN-CYCLE, CARBON METABOLISM, CO₂ FIXATION, ELECTRON-TRANSPORT, FRUCTOSE 2,6-BISPHOSPHATE, INVIVO, LIMITATION, PHOSPHORYLATION, SPINACH LEAF-DISKS, SUCROSE PHOSPHATE SYNTHASE

2210

Signora, L., N. Galtier, L. Skot, H. Lucas, and C.H. Foyer. 1998. Over-expression of sucrose phosphate synthase in *Arabidopsis thaliana* results in increased foliar sucrose/starch ratios and favours decreased foliar carbohydrate accumulation in plants after prolonged growth with CO₂ enrichment. *Journal of Experimental Botany* 49(321):669-680.

Arabidopsis thaliana ecotype Columbia was transformed with a maize sucrose phosphate synthase (SPS) cDNA under the control of the promoter for the small subunit of ribulose-1,5-bisphosphate carboxylase from tobacco (rbcS). The effects of SPS over-expression were compared in plants of the T-2 and T-3 generations grown either in air or with CO₂ enrichment (700 $\mu\text{mol l}^{-1}$) for either 4 or 10 weeks. Maximal extractable foliar SPS activities were three times those of the untransformed controls in the highest rbcS-SPS expressing line. In untransformed *Arabidopsis* leaves SPS activity was not subject to light/dark regulation, but was modified by incubation with either the inhibitor, orthophosphate, or the activator, mannose. Photosynthesis (A_{max}) values were similar in all lines grown in air. After 10 weeks of CO₂ enrichment a decrease in A_{max} in the untransformed controls, but not in the high SPS expressors, was observed. There was a strong correlation between the sucrose-to-starch ratio of the leaves and their SPS activity in both growth conditions. The total foliar carbohydrate contents of 4-week-old plants was similar in all lines whether plants were grown in air or with CO₂ enrichment. After 10 weeks growth the leaves of the high rbcS-SPS expressors accumulated much less total carbohydrate than untransformed control leaves in both growth conditions. It was concluded that SPS overexpression causes increased foliar sucrose/starch ratios in *Arabidopsis* leaves and favours decreased foliar carbohydrate contents when plants are grown for long periods with CO₂ enrichment.

KEYWORDS: ATMOSPHERIC CO₂, ELECTRON-TRANSPORT, ENZYME-ACTIVITIES, INORGANIC- PHOSPHATE, KINETIC-PROPERTIES, LIGHT-MODULATION, SINK REGULATION, SPINACH LEAVES, TRANSCRIPT LEVELS, TRANSGENIC PLANTS

2211

Sild, E., S. Younis, H. Pleijel, and G. Sellden. 1999. Effect of CO₂ enrichment on non-structural carbohydrates in leaves, stems and ears of spring wheat. *Physiologia Plantarum* 107(1):60-67.

Field-grown spring wheat (*Triticum aestivum* L, cv, Dragon) was exposed to ambient and elevated CO₂ concentrations (15 and 2 times ambient) in open-top chambers. Contents of non-structural carbohydrates were analysed enzymatically in leaves, stems and ears six times during the growing season. The impact of elevated CO₂ on wheat carbohydrates was non-significant in most harvests. However, differences in the carbohydrate contents due to elevated CO₂ were found in all plant compartments. Before anthesis, at growth stage (GS) 30 (the stem is 1 cm to the shoot apex), the plants grown in elevated CO₂ contained significantly more water soluble carbohydrates (WSC), fructans, starch and total non-structural carbohydrates (TNC) in the leaves in comparison with the plants grown in ambient CO₂. It is hypothesised that the plants from the treatments with elevated CO₂ were sink-limited at GS30. After anthesis, the leaf WSC and TNC contents of the plants from elevated CO₂ started to decline earlier than those of the plants from ambient CO₂. This may indicate that the leaves of plants grown in the chambers with elevated CO₂ senesced earlier. Elevated CO₂ accelerated grain development: 2 weeks after anthesis, the plants grown in elevated CO₂ contained significantly more starch and significantly less fructans in the ears compared to the plants grown in ambient CO₂. Elevated CO₂ had no effect on ear starch and TNC contents at the final harvest. Increasing the CO₂ concentration from 360 to 520 $\mu\text{mol mol}^{-1}$ had a larger effect on wheat nonstructural carbohydrates than the further increase from 520 to 680 $\mu\text{mol mol}^{-1}$. The results are discussed in relation to the effects of elevated CO₂ on yield and yield components.

KEYWORDS: ATMOSPHERIC CO₂, ELEVATED CO₂, FRUCTAN ACCUMULATION, GRAIN-YIELD, GROWTH, LONG-TERM, PHOTOSYNTHESIS, RESPONSES, TRITICUM-AESTIVUM L, WINTER-WHEAT

2212

Silver, W.L. 1998. The potential effects of elevated CO₂ and climate change on tropical forest soils and biogeochemical cycling. *Climatic Change* 39(2-3):337-361.

Tropical forests are responsible for a large proportion of the global terrestrial C flux annually for natural ecosystems. Increased atmospheric CO₂ and changes in climate are likely to affect the distribution of C pools in the tropics and the rate of cycling through vegetation and soils. In this paper, I review the literature on the pools and fluxes of carbon in tropical forests, and the relationship of these to nutrient cycling and climate. Tropical moist and humid forests have the highest rates of annual net primary productivity and the greatest carbon flux from soil respiration globally. Tropical dry forests have lower rates of carbon circulation, but may have greater soil organic carbon storage, especially at depths below 1 meter. Data from tropical elevation gradients were used to examine the sensitivity of biogeochemical cycling to incremental changes in temperature and rainfall. These data show significant positive correlations of litterfall N concentrations with temperature and decomposition rates. Increased atmospheric CO₂ and changes in climate are expected to alter carbon and nutrient allocation patterns and storage in tropical forest. Modeling and experimental studies suggest that even a small increase in temperature and CO₂ concentrations results in more rapid decomposition rates, and a large initial CO₂ efflux from moist tropical soils. Soil P limitation or reductions in C:N and C:P ratios of litterfall could eventually limit the size of this flux. Increased frequency of fires in dry forest and hurricanes in moist and humid forests are expected to reduce the ecosystem carbon storage capacity over longer time periods.

KEYWORDS: AMAZONIAN RAINFOREST, GLOBAL CARBON-CYCLE, LITTER DECOMPOSITION, LOA ENVIRONMENTAL MATRIX, LUQUILLO EXPERIMENTAL FOREST, MULU NATIONAL PARK, NUTRIENT AVAILABILITY, ORGANIC-MATTER, PUERTO-RICO, TERRESTRIAL ECOSYSTEMS

2213

Silvola, J., and U. Ahlholm. 1993. Effects of CO₂ concentration and nutrient status on growth, growth rhythm and biomass partitioning in a willow, *Salix phylicifolia*. *Oikos* 67(2):227-234.

Cuttings of the willow *Salix phylicifolia* were grown in pots containing moist organic-rich soil for four months in closed chambers at 4 CO₂ concentrations (300, 500, 700, 1000 ppm) and 4 nutrient levels (fertilization of 0, 100, 500, 1000 kg ha⁻¹ monthly). The plants received natural light, but the average temperature was 3-6-degrees-C higher than out of doors. Both CO₂ concentration and fertilization affected biomass production. The average increase caused by CO₂ enhancement being approx. 100%. Nutrient level had a considerable effect on the increased biomass production achieved by CO₂ enhancement, since the increase was minimal at lower nutrient levels. At the same time the effect of fertilization was dependent on the CO₂ concentration, the production increase caused by fertilization being much less at 300 ppm than at the other CO₂ concentrations. CO₂ concentration and fertilization had the opposite effects on biomass partitioning, a higher nutrient level increasing the proportion of the biomass located in the stems and a higher CO₂ concentration that in the roots. Both fertilization and CO₂ concentration affected the growth rhythm, a high CO₂/nutrient ratio leading to a shorter growing season and a low ratio to a longer one.

KEYWORDS: ATMOSPHERIC CARBON-DIOXIDE, DRY-MATTER

PRODUCTION, ELEVATED CO₂, ENRICHMENT, INCREASE, NITROGEN, PHOTOSYNTHETIC RATE, SEEDLINGS, SENESCENCE, TREES

2214

Silvola, J., and U. Ahlholm. 1995. Combined effects of CO₂ concentration and nutrient status on the biomass production and nutrient-uptake of birch seedlings (*Betula pendula*). *Plant and Soil* 169:547-553.

Birch seedlings (*Betula pendula*) were grown for four months in a greenhouse at three nutrient levels (fertilization of 0, 100 and 500 kg ha⁻¹ monthly) and at four CO₂ concentrations (350, 700, 1050 and 1400 ppm). The effect of CO₂ concentration on the biomass production depended on the nutrient status. When mineralization of the soil material was the only source of nutrients (0 kg ha⁻¹), CO₂ enhancement reduced the biomass production slightly, whereas the highest production increase occurred at a fertilization of 100 kg ha⁻¹, being over 100% between 350 and 700 ppm CO₂. At 500 kg ha⁻¹ the production increase was smaller, and the production decreased beyond a CO₂ concentration of 700 ppm. The CO₂ concentration had a slight effect on the biomass distribution, the leaves accounting for the highest proportion at the lowest CO₂ concentration (350 ppm). An increase in nutrient status led to a longer growth period and increased the nutrient concentrations in the plants, but the CO₂ concentration had no effect on the growth rhythm and higher CO₂ reduced the nutrient concentrations.

KEYWORDS: CARBON DIOXIDE, ELEVATED CO₂, ENRICHMENT, GROWTH, MARSH, NUTRITION, PHOTOSYNTHESIS, RESPONSES, SIZE, TEMPERATURE

2215

Simard, S.W., D.M. Durall, and M.D. Jones. 1997. Carbon allocation and carbon transfer between *Betula papyrifera* and *Pseudotsuga menziesii* seedlings using a C-13 pulse-labeling method. *Plant and Soil* 191(1):41-55.

Here we describe a simple method for pulse-labeling tree seedlings with (CO₂(gas)-C-13), and then apply the method in two related experiments: (i) comparison of carbon allocation patterns between *Betula papyrifera* Marsh. and *Pseudotsuga menziesii* (Mirb.) France, and (ii) measurement of one-way belowground carbon transfer from *B. papyrifera* to *P. menziesii*. Intraspecific carbon allocation patterns and interspecific carbon transfer both influence resource allocation, and consequently development, in mixed communities of *B. papyrifera* and *P. menziesii*. In preparation for the two experiments, we first identified the appropriate (CO₂(gas)-C-13) pulse-chase regime for labeling seedlings: a range of pulse (100-mL and 200-mL 99 atom% (CO₂(gas)-C-13)) and chase (0, 3 and 6 d) treatments were applied to one year-old *B. papyrifera* and *P. menziesii* seedlings. The amount of (CO₂-C-13) fixed immediately after 1.5 h exposure was greatest for both *B. papyrifera* (40.8 mg excess C-13) and *P. menziesii* (22.9 mg excess C-13) with the 200-mL pulse, but higher C-13 loss and high sample variability resulted in little difference in excess C-13 content between pulse treatments after 3 d for either species. The average excess C-13 root/shoot ratio of *B. papyrifera* and *P. menziesii* changed from 0.00 immediately following the pulse to 0.61 and 0.87 three and six days later, which reflected translocation of 75% of fixed isotope out of foliage within 3 d following the pulse and continued enrichment in fine roots over 6 d. Based on these results, the 100-mL CO₂(gas) and 6-d chase were considered appropriate for the carbon allocation and belowground transfer experiments. In the carbon allocation experiment, we found after 6 d that *B. papyrifera* allocated 49% (average 9.5 mg) and *P. menziesii* 41% (average 5.8 mg) of fixed isotope to roots, of which over 55% occurred in fine roots in both species. Species differences in isotope allocation patterns paralleled differences in tissue biomass distribution. The greater pulse labeling

efficiency of *B. papyrifera* compared to *P. menziesii* was associated with its two-fold and 13-fold greater leaf and whole seedling net photosynthetic rates, respectively, 53% greater biomass, and 35% greater root/shoot ratio. For the carbon transfer experiment, *B. papyrifera* and *P. menziesii* were grown together in laboratory rootboxes, with their roots intimately mingled. A pulse of 100 mL (CO₂(gas)-C-13) was applied to paper birch and one-way transfer to neighboring *P. menziesii* was measured after 6 d. Of the excess C-13 fixed by *B. papyrifera*, 4.7% was transferred to neighboring *P. menziesii*, which distributed the isotope evenly between roots and shoots. Of the isotope received by *P. menziesii*, we estimated that 93% was taken up through belowground pathways, and the remaining 7% taken up by foliage as (CO₂(gas)-C-13) respired by *B. papyrifera* shoots. These two experiments indicate that *B. papyrifera* fixes more total carbon and allocates a greater proportion to its root system than does *P. menziesii*, giving it a competitive edge in resource gathering; however, below-ground carbon sharing is of sufficient magnitude that it may help ensure co-existence of the two species in mixed communities.

KEYWORDS: BIRCH, CO₂, GROWTH, HYPHAE, PHOTOSYNTHESIS, PLANTS

2216

Simola, L.K., J. Lemmetyinen, and A. Santanen. 1992. Lignin release and photomixotrophism in suspension-cultures of *Picea abies*. *Physiologia Plantarum* 84(3):374-379.

The effect of different concentrations of sucrose (0-4%) and of two growth regulators (0-50- μ M 2,4-D and 0-25- μ M kinetin) was tested on growth and chlorophyll content of suspension cultures of *Picea abies* (L.) Karst. originating from chlorophyllous embryo callus in an elevated CO₂ (2%) atmosphere. A continuous chlorophyllous suspension culture was achieved on a medium containing 2% sucrose and a low level of organic nitrogen (0.25 mM arginine and 0.5 mM glutamine) supplemented with 2,4-D (0.5- μ M) and kinetin (2.5- μ M). The same medium with 4% sucrose gave the best growth response, but a negative correlation between chlorophyll level and growth was observed. The chlorophyllous cultures grew slowly in a medium with low (0.5%) sucrose or without any carbohydrate source, suggesting photomixotrophism. A high concentration of kinetin inhibited both growth and chlorophyll synthesis. Release of lignin into the nutrient medium was observed in several experiments, especially in slow-growing cultures supplemented with sucrose. Only a few successive passages of suspensions that produced lignin could be cultured before cell death. The cultures releasing lignin may be unique for studies on synthesis and biodegradation of this very complex compound.

KEYWORDS: CALLUS LINES, CELL-CULTURES, DIFFERENTIATION, ESTABLISHMENT, FINE-STRUCTURE, GROWTH, LIGNIFICATION, MEGAGAMETOPHYTE, NICOTIANA-TABACUM, SPRUCE

2217

Simon, J.P. 1996. Molecular forms and kinetic properties of pyruvate, P-i dikinase from two populations of barnyard grass (*Echinochloa crus-galli*) from sites of contrasting climates. *Australian Journal of Plant Physiology* 23(2):191-199.

Plants from two populations of the C-4 barnyard grass (*Echinochloa crus-galli* (L.) Beauv.) from Quebec (QUE) and Mississippi (MISS) were acclimated under controlled conditions to 26/20 and 14/8 degrees C day/night. The apparent energy of activation (E(a)), K-m for pyruvate, V-max/K-m ratios, K-cat (substrate turnover number) and specific activity of pyruvate, P-i dikinase (PPDK, EC 2.7.9.1) were analysed from partially purified Sephadex G-25 extracts of PPDK from leaves and from highly purified PPDK. PPDK from both populations consisted of

one isomorph with the same electrophoretic mobility in polyacrylamide gels and similar molecular weights for the native enzyme (385 kDa) and for the subunit of the tetramer (94.8 kDa). No significant differences were observed for any of the kinetic properties of partially purified or purified PPDK or for the specific activity per mg protein of purified PPDK extracted from plants of the two populations and acclimated to the two thermoperiods. Net photosynthetic rates (Ps) were positively correlated with PPDK activity levels (E) but E/Ps ratios were lower than 1.0, ranging from 0.43 to 0.67. Results indicate that differences in activity levels, thermal properties and in the kinetics of light activation and dark inactivation of PPDK extracted from cold-acclimated MISS and QUE plants, as reported in earlier studies, are due to causes other than kinetic properties or electrophoretic characteristics of PPDK.

KEYWORDS: C-4 PHOTOSYNTHESIS, CO₂- ENRICHMENT, CRUSGALLI L BEAUV, ECOTYPES, ENZYME LEVEL, HIGHER-PLANTS, NADP+ -MALATE DEHYDROGENASE, PHOSPHOENOLPYRUVATE CARBOXYLASE, PURIFICATION, TEMPERATURE

2218

Sims, D.A., W.X. Cheng, Y.Q. Luo, and J.R. Seemann. 1999. Photosynthetic acclimation to elevated CO₂ in a sunflower canopy. *Journal of Experimental Botany* 50(334):645-653.

Sunflower canopies were grown in mesocosm gas exchange chambers at ambient and elevated CO₂ concentrations (360 and 700 ppm) and leaf photosynthetic capacities measured at several depths within each canopy. Elevated [CO₂] had little effect on whole-canopy photosynthetic capacity and total leaf area, but had marked effects on the distribution of photosynthetic capacity and leaf area within the canopy. Elevated [CO₂] did not significantly reduce the photosynthetic capacities per unit leaf area of young leaves at the top of the canopy, but it did reduce the photosynthetic capacities of older leaves by as much as 40%. This effect was not dependent on the canopy light environment since elevated [CO₂] also reduced the photosynthetic capacities of older leaves exposed to full sun on the south edge of the canopy. In addition to the effects on leaf photosynthetic capacity, elevated [CO₂] shifted the distribution of leaf area within the canopy so that more leaf area was concentrated near the top of the canopy. This change resulted in as much as a 50% reduction in photon flux density in the upper portions of the elevated [CO₂] canopy relative to the ambient [CO₂] canopy, even though there was no significant difference in the total canopy leaf area. This reduction in PFD appeared to account for leaf carbohydrate contents that were actually lower for many of the shaded leaves in the elevated as opposed to the ambient [CO₂] canopy. Photosynthetic capacities were not significantly correlated with any of the individual leaf carbohydrate contents. However, there was a strong negative correlation between photosynthetic capacity and the ratio of hexose sugars to sucrose, consistent with the hypothesis that sucrose cycling is a component of the biochemical signalling pathway controlling photosynthetic acclimation to elevated [CO₂].

KEYWORDS: ATMOSPHERIC CO₂, CARBON-DIOXIDE CONCENTRATION, GAS-EXCHANGE, GENE-EXPRESSION, GROWTH, LEAF, LIGHT, PLANTS, RIBULOSE-1:5-BISPHOSPHATE CARBOXYLASE, SOYBEAN LEAVES

2219

Sims, D.A., Y. Luo, and J.R. Seemann. 1998. Comparison of photosynthetic acclimation to elevated CO₂ and limited nitrogen supply in soybean. *Plant, Cell and Environment* 21(9):945-952.

Plants grown at elevated CO₂ often acclimate such that their photosynthetic capacities are reduced relative to ambient CO₂-grown plants. Reductions in synthesis of photosynthetic enzymes could result

either from reduced photosynthetic gene expression or from reduced availability of nitrogen-containing substrates for enzyme synthesis. Increased carbohydrate concentrations resulting from increased photosynthetic carbon fixation at elevated CO₂ concentrations have been suggested to reduce the expression of photosynthetic genes. However, recent studies have also suggested that nitrogen uptake may be depressed by elevated CO₂, or at least that it is not increased enough to keep pace with increased carbohydrate production. This response could induce a nitrogen limitation in elevated-CO₂ plants that might account for the reduction in photosynthetic enzyme synthesis. If CO₂ acclimation were a response to limited nitrogen uptake, the effects of elevated CO₂ and limiting nitrogen supply on photosynthesis and nitrogen allocation should be similar. To test this hypothesis we grew non-nodulating soybeans at two levels each of nitrogen and CO₂ concentration and measured leaf nitrogen contents, photosynthetic capacities and Rubisco contents. Both low nitrogen and elevated CO₂ reduced nitrogen as a percentage of total leaf dry mass but only low nitrogen supply produced significant decreases in nitrogen as a percentage of leaf structural dry mass. The primary effect of elevated CO₂ was to increase non-structural carbohydrate storage rather than to decrease nitrogen content. Both low nitrogen supply and elevated CO₂ also decreased carboxylation capacity (V_{cmax}) and Rubisco content per unit leaf area. However, when V_{cmax} and Rubisco content were expressed per unit nitrogen, low nitrogen supply generally caused them to increase whereas elevated CO₂ generally caused them to decrease. Finally, elevated CO₂ significantly increased the ratio of RuBP regeneration capacity to V_{cmax} whereas neither nitrogen supply nor plant age had a significant effect on this parameter. We conclude that reductions in photosynthetic enzyme synthesis in elevated CO₂ appear not to result from limited nitrogen supply but instead may result from feedback inhibition by increased carbohydrate contents.

KEYWORDS: ATMOSPHERIC CO₂, C-3 PLANTS, CARBON DIOXIDE, GAS-EXCHANGE, GROWTH, LEAVES, PARTIAL-PRESSURE, RIBULOSE-1,5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, RUBISCO, SMALL-SUBUNIT

2220

Sims, D.A., Y. Luo, and J.R. Seemann. 1998. Importance of leaf versus whole plant CO₂ environment for photosynthetic acclimation. *Plant, Cell and Environment* 21(11):1189-1196.

The reduction of photosynthetic capacity in many plants grown at elevated CO₂ is thought to result from a feedback effect of leaf carbohydrates on gene expression. Carbohydrate feedback at elevated CO₂ could result from limitations on carbohydrate utilization at many different points, for example export of triose phosphates from the chloroplast, sucrose synthesis and phloem loading, transport in the phloem, unloading of the phloem at the sinks, or utilization for growth of sinks. To determine the relative importance of leaf versus whole plant level limitations on carbohydrate utilization at elevated CO₂, and the possible effects on the regulation of photosynthetic capacity, we constructed a treatment system in which we could expose single, attached, soybean leaflets to CO₂ concentrations different from those experienced by the rest of the plant. The single leaflet treatments had dramatic effects on the carbohydrate contents of the treated leaflets. However, photosynthetic capacity and rubisco content were unaffected by the individual leaflet treatment and instead were related to the whole plant CO₂ environment, despite the fact that the CO₂ environment around the rest of the plant had no significant effect on the total non-structural carbohydrate (TNC) contents of the treated leaflets. These results necessitate a re-evaluation of the response mechanisms to CO₂ as well as some of the methods used to test these responses. We propose mechanisms by which sink strength could influence leaf physiology independently of changes in carbohydrate accumulation.

KEYWORDS: CARBON ASSIMILATION, ELEVATED CO₂, GAS-

EXCHANGE, GENE-EXPRESSION, IN-BAG EXPERIMENT, LEAVES, PHLOEM TRANSPORT, RIBULOSE-1,5-BISPHOSPHATE CARBOXYLASE, SCOTS PINE, SINK REGULATION

2221

Sims, D.A., J.R. Seemann, and Y. Luo. 1998. The significance of differences in the mechanisms of photosynthetic acclimation to light, nitrogen and CO₂ for return on investment in leaves. *Functional Ecology* 12(2):185-194.

1. We report changes in photosynthetic capacity of leaves developed in varying photon flux density (PFD), nitrogen supply and CO₂ concentration. We determined the relative effect of these environmental factors on photosynthetic capacity per unit leaf volume as well as the volume of tissue per unit leaf area. We calculated resource-use efficiencies from the photosynthetic capacities and measurements of leaf dry mass, carbohydrates and nitrogen content. 2. There were clear differences between the mechanisms of photosynthetic acclimation to PFD, nitrogen supply and CO₂. PFD primarily affected volume of tissue per unit area whereas nitrogen supply primarily affected photosynthetic capacity per unit volume. CO₂ concentration affected both of these parameters and interacted strongly with the PFD and nitrogen treatments. 3. Photosynthetic capacity per unit carbon invested in leaves increased in the low PFD, high nitrogen and low CO₂ treatments. Photosynthetic capacity per unit nitrogen was significantly affected only by nitrogen supply. 4. The responses to low PFD and low nitrogen appear to function to increase the efficiency of utilization of the limiting resource. However, the responses to elevated CO₂ in the high PFD and high nitrogen treatments suggest that high CO₂ can result in a situation where growth is not limited by either carbon or nitrogen supply. Limitation of growth at elevated CO₂ appears to result from internal plant factors that limit utilization of carbohydrates at sinks and/or transport of carbohydrates to sinks.

KEYWORDS: ALOCASIA-MACRORRHIZA, C-3 PLANTS, CARBON BALANCE, ELEVATED CO₂, ENRICHMENT, GROWTH, LEAF ANATOMY, PHOTON FLUX DENSITIES, SCALING SUN, WHOLE-PLANT PERFORMANCE

2222

Sims, D.A., J.R. Seemann, and Y.Q. Luo. 1998. Elevated CO₂ concentration has independent effects on expansion rates and thickness of soybean leaves across light and nitrogen gradients. *Journal of Experimental Botany* 49(320):583-591.

The rate and extent of leaf thickness and development are important determinants of plant photosynthetic capacity. The interactive effects of photon flux density (PFD), nitrogen supply and CO₂ concentration on leaf expansion rate were measured as well as final leaf size and thickness of soybean. Leaf thickness and final area were not correlated with leaf relative expansion rate (RER) suggesting that these parameters are controlled by different mechanisms and that final leaf dimensions are determined by the duration rather than the rate of leaf expansion. Carbohydrate supply did not explain the variation in leaf RER since RER increased with increasing CO₂ concentration, but decreased with increasing PFD. Leaf thickness and final area were related to resource supply but not in a simple fashion. Both positive and negative correlations between leaf thickness and carbohydrate and nitrogen concentrations were obtained depending on the environmental variable responsible for the variation. In contrast, there was a simple proportional relationship between whole plant relative growth rate and a correlate of leaf thickness (leaf water content per unit area), suggesting that leaf thickness responds to the balanced supply of all resources, in the same fashion as RGR, rather than to any individual resource.

KEYWORDS: ACCLIMATION, ANATOMY, CARBON, ENRICHMENT,

2223

Sinclair, T.R. 1992. Mineral-nutrition and plant-growth response to climate change. *Journal of Experimental Botany* 43(253):1141-1146.

The limiting factor concept has often been used to describe plant growth responses to altered availability of resources. However, even preliminary experiments, where atmospheric CO₂ concentrations and solution mineral concentrations were varied, demonstrated that a more complex concept was required to interpret the potential effects of climate change and mineral availability on plant growth. It is proposed that these resources for plant growth may be better viewed as simultaneously limiting. Further, in considering the limitation in plant growth to mineral nutrition it is important to consider both the solution concentration and the total amount of the individual minerals available to the plant. Sustaining a positive response to increased CO₂ concentration, for example, requires an increase in plant uptake of the total amount of minerals. Consequently, it is very difficult to predict the plant growth response to climate change because of the large uncertainty about mineral availability. On the one hand, increased CO₂ concentrations should stimulate nitrogen fixation by both free-living organisms and symbiotic systems, and improve soil properties for mineral availability as a result of increased organic matter deposition in the soil. On the other hand, increased temperature and altered rainfall patterns may result in increased losses of soil minerals. Even the direction in the net change in available soil minerals is unclear. Realistic evaluations of the effects of climate change on plant growth will be challenged to contend with the large uncertainty and complexities in understanding mineral availability and plant mineral nutrition.

KEYWORDS: CARBON-DIOXIDE ENRICHMENT, CO₂-ENRICHMENT, NET NITROGEN MINERALIZATION, ROOT NODULE ACTIVITY, SEED YIELD, SOILS

2224

Sinclair, T.R., and N.G. Seligman. 1995. Global environment change and simulated forage quality of wheat .1. Nonstressed conditions. *Field Crops Research* 40(1):19-27.

Projected changes in the global environment may affect both the quantity and quality of grain and forage mass produced and harvested in that environment. Quality is a major factor in determining the value of a forage crop as feed for ruminants. The objective of this study was to make a preliminary assessment of potential changes in the quantity and quality of forage as measured by [N] and leaf:stem of an annual, temperate climate C-3 forage crop grown under nonstressed conditions. Starting with a relatively simple, well-checked mechanistic model of wheat, adaptations were added to estimate changes in forage attributes. Increased temperature influenced both yield and nutritive value, mainly through changes in ontological development rates. Elevated,atmospheric [CO₂] resulted in greater mass accumulation, but with lower leaf:stem and [N]. The combined effect of increased temperature and elevated [CO₂] was to decrease slightly forage yield and to increase the forage nutritive value. These compensating effects of higher temperature and elevated [CO₂] could be modified by interactions between [CO₂] and the chemical composition and cell wall structure of forage plants. Analysis of such subtle interaction requires considerable experimental amplification.

KEYWORDS: CARBON DIOXIDE, CO₂- ENRICHMENT, DRY-MATTER, ELEVATED CO₂, GROWTH, NITROGEN, SPRING WHEAT, TEMPERATURE, WINTER-WHEAT, YIELD

2225

Singer, A., A. Eshel, M. Agami, and S. Beer. 1994. The contribution of aerenchymal co₂ to the photosynthesis of emergent and submerged culms of scirpus-lacustris and cyperus- papyrus. *Aquatic Botany* 49(2-3):107-116.

In this work it was investigated whether sediment-derived aerenchymal CO₂ could be utilized for photosynthesis in the culms of the two emergent aquatic macrophytes *Scirpus lacustris* L. (a C-3 plant) and *Cyperus papyrus* L. (a C-4 plant). Aerenchymal CO₂ concentrations within the submerged parts of the culms were found to be 30 000-50 000, $\mu\text{mol l}^{-1}$, and ca. 800 $\mu\text{mol l}^{-1}$ in the emergent parts of *Scirpus lacustris* and 2000 $\mu\text{mol l}^{-1}$ in *Cyperus papyrus*. These concentrations tended to be lower during the day in *Cyperus*, while no clear diurnal pattern was observed for *Scirpus*. Photosynthetic rates based on fixation of external or internal CO₂ were measured in situ by providing (CO₂)-C-14 either externally or from the aerenchyma (by supplying C-14-labelled CO₂ through test-tubes attached to excised culms). The results showed that the contribution of aerenchymal CO₂ to the total photosynthesis of emergent culms was less than 0.25% in both species. This has a rationale in that photosynthetic rates of both species were saturated at the ambient air CO₂ concentration, but it remains unclear why CO₂ does not diffuse towards the photosynthesizing tissues. By contrast, internal CO₂ appeared to be the only source of inorganic carbon used for photosynthesis of young submerged green culms. It is thus suggested that the aerenchyma, in addition to other functions, is important in providing sediment-derived CO₂ for photosynthesis in young shoots or culms if growing submerged, before they reach the water surface.

KEYWORDS: CARBON, ELEVATED ATMOSPHERIC CO₂, FLOW, TRIN EX STEUD

2226

Singh, B., and R.B. Stewart. 1991. Potential impacts of a CO₂-induced climate change using the GISS scenario on agriculture in quebec, canada. *Agriculture Ecosystems & Environment* 35(4):327-347.

This study examines the potential impacts of a climate change resulting from an effective doubling of atmospheric CO₂ on the potential and anticipated yields of a variety of agricultural crops including corn, soya, potatoes, wheat, phaseolus beans, sorghum, barley, oats, rapeseed and sunflowers and two horticultural crops namely apples and grapes, for southern Quebec. The GISS climate change scenario is used. Our results show that yields would increase for some crops such as corn, soybeans, potatoes, phaseolus beans and sorghum and would decrease for the cereal and oilseed crops, namely wheat, barley, oats, sunflowers and rapeseed. Production opportunities for apples and grapes are enhanced. Also it would seem that the more northerly regions of Abitibi-Temiscamingue and Lac St-Jean would benefit most, in terms of agriculture, from a CO₂-induced climate change.

KEYWORDS: BALANCE, CARBON DIOXIDE, CO₂, COMPONENTS, CROP, CYCLE, GENERAL-CIRCULATION MODEL, SENSITIVITY, WHEAT, YIELD

2227

Singh, T., and E.E. Wheaton. 1991. Boreal forest sensitivity to global warming - implications for forest management in western interior canada. *The Forestry Chronicle* 67(4):342-348.

Unmitigated global warming due to the enhanced greenhouse effect could have significant impacts on the boreal forest in interior western Canada. Increases in annual temperature of 3 to 7-degrees-C are projected for Alberta under a 2 x CO₂ scenario by 2030-2050 A.D. Such an unprecedented rate of change has many short- and long-term

implications for forest management and for industries. As the boreal forest is highly sensitive to climatic changes, foresters need to develop a set of safe strategies to minimize the negative impacts and maximize the benefits of these changes.

2228

Slafer, G.A. 1995. Wheat development as affected by radiation at two temperatures. *Journal of Agronomy and Crop Science-Zeitschrift Fur Acker Und Pflanzenbau* 175(4):249-263.

A wheat cultivar (Condor) was grown in two experiments (thermal regimes 18/13 and 21/16 degrees C) under low (298 $\mu\text{mol m}^{-2} \text{s}^{-1}$) radiation regimes during either an early phase from seedling emergence to terminal spikelet initiation (S-1), a late phase from terminal spikelet initiation to anthesis (S-2), or for the full period from seedling emergence to anthesis (S-12), or high (560 $\mu\text{mol m}^{-2} \text{s}^{-1}$) radiation throughout the growing period (S-0) to determine whether developmental events are affected by radiation. The main developmental events considered in this study were the timing of terminal spikelet initiation and anthesis, the final number of leaf and spikelet primordia initiated in the apex and the rate of leaf appearance. Number of grains per spike and culm height were also measured. The duration of each phenophase was not affected by radiation intensity. Temperature affected the rate of wheat development, but the acceleration of development due to temperature during the seedling emergence-terminal spikelet initiation phase only slightly reduced (from 24.8 to 23.2 days). Differences in time from terminal spikelet initiation to anthesis were greater than in the earlier phases, having been the duration reduced from 24.6 to 20.0 days due to high temperature. Associated with the lack of effect of radiation on phasic development and the negligible effect of temperature on the duration of the early phases of development, final leaf number was practically unchanged in this study by either the radiation level or the growing temperature. Thus, radiation did not affect the rate of leaf initiation. The number of spikelets was affected by neither the treatments nor the thermal environment. The rates of leaf appearance were accelerated by temperature. Radiation, on the other hand, did not significantly alter the rates of leaf appearance in any of the treatments. As expected from many sources in the literature, the number of grains per spike was significantly affected by radiation during the phase from terminal spikelet initiation to anthesis. Due to the lack of significant effects of radiation on the developmental patterns of wheat, the changes in number of grains per spike were due to changes in the number of grains born in each spikelet. The results of the present study were compared with others available in the literature on the effects (or lack of them) of radiation and CO₂ concentration on phasic development, plastochron and phyllochron in wheat to reach the general conclusion that the rate of developmental events in wheat, in contrast to other plants, is almost completely independent of the availability of assimilates, with a possible exception for the Equatorial latitudes.

KEYWORDS: BASE TEMPERATURE, CARBON-DIOXIDE ENRICHMENT, CO₂- ENRICHMENT, GRAIN-YIELD, GROWTH, PHOTOPERIOD, SPIKELET NUMBER, SPRING WHEAT, WATER-STRESS, WINTER-WHEAT

2229

Slafer, G.A., and H.M. Rawson. 1997. CO₂ effects on phasic development, leaf number and rate of leaf appearance in wheat. *Annals of Botany* 79(1):75-81.

It has been predicted that the concentration of CO₂ in the air could double during the 21st century. Though it is recognized that CO₂-doubling could increase yield through its effects on plant photosynthesis and stomatal behaviour, it is unclear whether CO₂-doubling will change phasic development in wheat. A phytotron study was conducted with

two contrasting cultivars of wheat, Condor (spring) and Cappelle Desprez (winter), to determine whether development is affected by a season-long exposure to 360 and 720 ppmv CO₂. Plants were vernalized for 50 d (8/4 degrees C, 8 h photoperiod) before their exposure to the CO₂ treatments. There were significant differences between cultivars in the duration of different phenophases as well as in the final number of leaves. However, CO₂ concentration had no effect in either cultivar on the duration of the early developmental phase to terminal spikelet initiation, or on the final number of leaves, though CO₂-doubling did slightly increase the later phase from terminal spikelet initiation to heading in Cappelle Desprez. Condor and Cappelle Desprez also differed markedly in the dynamics of leaf appearance. While the former had a constant rate of leaf appearance throughout development, the latter had a fast rate initially (between leaves 1 and 7), similar to that of Condor, which was followed by a slower rate after the appearance of leaf 7. Overall, CO₂-doubling did not significantly affect the rates of leaf appearance nor the shape of the relationship. Phyllochron for the first seven leaves was the same for both CO₂ concentrations. However, the change in phyllochron associated with CO₂-doubling for leaves 7-12 in Cappelle Desprez, although quite small (4%), accounts for part of the slightly increased duration of the phase from terminal spikelet initiation to heading under high CO₂ concentration in that cultivar. We conclude that CO₂ concentration does not influence development in wheat to a degree relevant to agronomy. (C) 1997 Annals of Botany Company

KEYWORDS: ATMOSPHERIC CO₂, BASIC DEVELOPMENT RATE, CARBON-DIOXIDE ENRICHMENT, ELEVATED CO₂, GROWTH, PHOTOPERIOD, SOWING DATE, SPRING WHEAT, TEMPERATURE, WINTER-WHEAT

2230

Smart, D.R., N.J. Chatterton, and B. Bugbee. 1994. The influence of elevated CO₂ on nonstructural carbohydrate distribution and fructan accumulation in wheat canopies. *Plant, Cell and Environment* 17(4):435-442.

We grew 2.4 m² wheat canopies in a large growth chamber under high photosynthetic photon flux (1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and using two CO₂ concentrations, 360 and 1200 $\mu\text{mol mol}^{-1}$. Photosynthetically active radiation (400-700 nm) was attenuated slightly faster through canopies grown in 360 $\mu\text{mol mol}^{-1}$ than through canopies grown in 1200 $\mu\text{mol mol}^{-1}$, even though high-CO₂ canopies attained larger leaf area indices. Tissue fractions were sampled from each 5-cm layer of the canopies. Leaf tissue sampled from the tops of canopies grown in 1200 $\mu\text{mol mol}^{-1}$ accumulated significantly more total non-structural carbohydrate, starch, fructan, sucrose, and glucose (p less than or equal to 0.05) than for canopies grown in 360 $\mu\text{mol mol}^{-1}$. Non-structural carbohydrate did not significantly increase in the lower canopy layers of the elevated CO₂ treatment. Elevated CO₂ induced fructan synthesis in all leaf tissue fractions, but fructan formation was greatest in the uppermost leaf area. A moderate temperature reduction of 10-degrees-C over 5 d increased starch, fructan and glucose levels in canopies grown in 1200 $\mu\text{mol mol}^{-1}$, but concentrations of sucrose and fructose decreased slightly or remained unchanged. Those results may correspond with the use of fructosyl-residues and release of glucose when sucrose is consumed in fructan synthesis.

KEYWORDS: CARBONDIOXIDE, LEAVES, LOLIUM-TEMULENTUM L, METABOLISM, PHOTOSYNTHESIS, PLANTS, RESPIRATION, SUCROSE, TEMPERATURES

2231

Smart, D.R., K. Ritchie, A.J. Bloom, and B.B. Bugbee. 1998. Nitrogen balance for wheat canopies (Triticum aestivum cv. Veery 10) grown under elevated and ambient CO₂ concentrations. *Plant, Cell and Environment* 21(8):753-763.

We examined the hypothesis that elevated CO₂ concentration would increase NO₃⁻ absorption and assimilation using intact wheat canopies (Triticum aestivum cv, Veery 10), Nitrate consumption, the sum of plant absorption and nitrogen loss, was continuously monitored for 23 d following germination under two CO₂ concentrations (360 and 1000 $\mu\text{mol mol}^{-1}$ CO₂) and two root zone NO₃⁻ concentrations (100 and 1000 mmol m^{-3} NO₃⁻). The plants were grown at high density (1780 m^{-2}) in a 28 m³ controlled environment chamber using solution culture techniques. Wheat responded to 1000 $\mu\text{mol mol}^{-1}$ CO₂ by increasing carbon allocation to root biomass production. Elevated CO₂ also increased root zone NO₃⁻ consumption, but most of this increase did not result in higher biomass nitrogen. Rather, nitrogen loss accounted for the greatest part of the difference in NO₃⁻ consumption between the elevated and ambient [CO₂] treatments. The total amount of NO₃⁻-N absorbed by roots or the amount of NO₃⁻-N assimilated per unit area did not significantly differ between elevated and ambient [CO₂] treatments. Instead, specific leaf organic nitrogen content declined, and NO₃⁻ accumulated in canopies growing under 1000 $\mu\text{mol mol}^{-1}$ CO₂. Our results indicated that 1000 $\mu\text{mol mol}^{-1}$ CO₂ diminished NO₃⁻ assimilation. If NO₃⁻ assimilation were impaired by high [CO₂], then this offers an explanation for why organic nitrogen contents are often observed to decline in elevated [CO₂] environments.

KEYWORDS: ASSIMILATION, ATMOSPHERIC CO₂, BARLEY, CARBON-DIOXIDE ENRICHMENT, LEAVES, NITRATE REDUCTASE-ACTIVITY, PLANT GROWTH, TEMPERATURE, TOMATO, WINTER-WHEAT

2232

Smart, D.R., K. Ritchie, J.M. Stark, and B. Bugbee. 1997. Evidence that elevated CO₂ levels can indirectly increase rhizosphere denitrifier activity. *Applied and Environmental Microbiology* 63(11):4621-4624.

We examined the influence of elevated CO₂ concentration on denitrifier enzyme activity in wheat rhizoplanes by using controlled environments and solution culture techniques. Potential denitrification activity was from 3 to 24 times higher on roots that were grown under an elevated CO₂ concentration of 1,000 μmol of CO₂ mol^{-1} than on roots grown under ambient levels of CO₂. Nitrogen loss, as determined by a nitrogen mass balance, increased with elevated CO₂ levels in the shoot environment and with a high NO₃⁻ concentration in the rooting zone. These results indicated that aerial CO₂ concentration can play a role in rhizosphere denitrifier activity.

KEYWORDS: AMMONIA, ENVIRONMENT, EXCHANGE, PLANTS, RICE, SOIL DENITRIFICATION, WHEAT

2233

Smeekens, S. 1998. Sugar regulation of gene expression in plants. *Current Opinion in Plant Biology* 1(3):230-234.

The molecular details of sugar sensing and sugar-mediated signal transduction pathways are unclear but recent results suggest that hexokinase functions as an important plant sugar sensor in a way that is similar to that found in yeast. The use of mutants in Arabidopsis defective in specific signaling steps is of particular importance because these give access to the genes encoding components in the signaling pathways. In addition, the physiological analysis of such mutants may reveal the interaction of sugar-induced signaling pathways and those induced by other stimuli such as environmental or biotic stress.

KEYWORDS: ARABIDOPSIS-THALIANA, BETA-AMYLASE, CHENOPODIUM-RUBRUM, ELEVATED CO₂, GLUCOSE, INVERTASE, SACCHAROMYCES- CEREVISIAE, SIGNAL-TRANSDUCTION, SUCROSE EXPORT, TISSUE-SPECIFIC EXPRESSION

2234

Smernoff, D.T., J. Gale, B.A. MacIer, and J. Reuveni. 1993. Inhibition of photosynthesis in duckweed by elevated CO₂ concentration is rapid and is not offset by a temperature- induced increase in metabolic-rate. *Photosynthetica* 28(1):17-28.

The rates of net photosynthesis (P(N)), respiration and growth of Lemna gibba L. were measured as functions of time across ranges of temperature, irradiance and carbon dioxide concentrations. P(N) on an area basis increased with temperature up to 30-degrees-C but decreased dramatically with a few hours of exposure to elevated CO₂, when reported on a dry mass basis. Reductions in the apparent quantum efficiency, photosynthetic capacity and the affinity of ribulose- 1,5-bisphosphate carboxylase/oxygenase for CO₂ were observed for plants grown at elevated CO₂. Starch concentration was not significantly affected by elevated CO₂. Although elevated temperature increased metabolic activity, it only partially alleviated the inhibition of P(N). L. gibba exhibits a characteristic C3-type response to elevated CO₂ and the methodology described is useful for further elucidating the mechanism of photosynthetic acclimation to elevated CO₂.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, CARBOXYLASE, CULTIVATION, DESERT CONDITIONS, ENRICHMENT, GROWTH, HIGHATMOSPHERIC CO₂, LEMNA-GIBBA, PHOTORESPIRATION

2235

Smit, B., and Y.L. Cai. 1996. Climate change and agriculture in China. *Global Environmental Change-Human and Policy Dimensions* 6(3):205-214.

The implications of climate change for agriculture and food are global concerns, and they are very important for China. The country depends on an agricultural system which has evolved over thousands of years to intensively exploit environmental conditions. The pressures on the resource base are accentuated by the prospect of climate change. This paper synthesizes information from a variety of studies on Chinese agriculture and climate. Historical studies document the impacts of past climate changes and extremes, and the types of adjustments which have occurred, the vulnerability of Chinese agriculture to climate change. Climate change scenarios are assessed relative to the current distribution of agro-climatic regions and systems. Notwithstanding the enhancing effects of warming and elevated CO₂ levels, expected moisture deficits and uncertain changes in the timing and frequency of critical conditions indicate that there are serious threats to the stability and adaptability of China's food production system. Copyright (C) 1996 Elsevier Science Ltd

2236

Smith, P.H.D., and T.H. Jones. 1998. Effects of elevated CO₂ on the chrysanthemum leafminer, Chromatomyia syngenesiae: a greenhouse study. *Global Change Biology* 4(3):287-291.

Although feeding behaviour of Chromatomyia syngenesiae on plants grown in elevated CO₂ (ambient + 200ppm) was unaffected, leaf-miner development was slower in elevated compared to ambient CO₂ atmospheres. Pupal weight was lower at high CO₂ and correlated with the area of leaf mined; no such correlation existed in ambient CO₂. There appears to be no compensatory feeding by the leaf-miner for the reduced food quality of plants growing in elevated CO₂. The implications of these findings are discussed.

KEYWORDS: HERBIVORE INTERACTIONS

2237

Smith, R.B. 1992. Controlled-atmosphere storage of redcoat strawberry fruit. *Journal of the American Society for Horticultural Science* 117(2):260-264.

Strawberries (*Fragaria x ananassa* Duch.) cv. Redcoat were stored at several temperatures and for various intervals in controlled atmospheres (CA) containing 0% to 18% CO₂ and 15% to 21% O₂. Bioyield point forces recorded on the CA-stored fresh fruit indicated that the addition of CO₂ to the storage environment enhanced fruit firmness. Fruit kept under 15% CO₂ for 18 hours was 48% firmer than untreated samples were initially. Response to increasing CO₂ concentrations was linear. There was no response to changing O₂ concentrations. Maximum enhancement of firmness was achieved at a fruit temperature of 0°C; there was essentially no enhancement at 21°C. In some instances, there was a moderate firmness enhancement as time in storage increased. Carbon dioxide acted to reduce the quantity of fruit lost due to rot. Fruit that was soft and bruised after harvest became drier and firmer in a CO₂-enriched environment.

KEYWORDS: DECAY, QUALITY

2238

Smith, R.B., and L.J. Skog. 1992. Postharvest carbon-dioxide treatment enhances firmness of several cultivars of strawberry. *Hortscience* 27(5):420-421.

Various cultivars of strawberry (*Fragaria x ananassa* Duch.) were stored for 42 h under an atmosphere of 15% CO₂ to determine whether their firmness would be enhanced. Compared to initial samples and stored control samples, enhanced firmness was found in 21 of the 25 cultivars evaluated. The CO₂ had no effect on color, as measured by Hunter 'L', 'a' and 'b', or on soluble solids concentration (SSC) or pH. There were significant differences among cultivars in firmness; Hunter color 'L', 'a', and 'b'; SSC; and pH.

KEYWORDS: ATMOSPHERES, QUALITY

2239

Smith, T.M., W.P. Cramer, R.K. Dixon, R. Leemans, R.P. Neilson, and A.M. Solomon. 1993. The global terrestrial carbon-cycle. *Water, Air, and Soil Pollution* 70(1-4):19-37.

There is great uncertainty with regard to the future role of the terrestrial biosphere in the global carbon cycle. The uncertainty arises from both an inadequate understanding of current pools and fluxes as well as the potential effects of rising atmospheric concentrations of CO₂ on natural ecosystems. Despite these limitations, a number of studies have estimated current and future patterns of terrestrial carbon storage. Future estimates focus on the effects of a climate change associated with a doubled atmospheric concentration of CO₂. Available models for examining the dynamics of terrestrial carbon storage and the potential role of forest management and landuse practices on carbon conservation and sequestration are discussed.

KEYWORDS: CLIMATE CHANGE, ECOSYSTEMS, ELEVATED CO₂ CONCENTRATIONS, ESTUARINE MARSH, FORESTS, GENERAL-CIRCULATION MODEL, INCREASE, SENSITIVITY, SOILS, STORAGE

2240

Smith, T.M., R. Leemans, and H.H. Shugart. 1992. Sensitivity of terrestrial carbon storage to CO₂-induced climate change - comparison of 4 scenarios based on general- circulation models. *Climatic Change* 21(4):367-384.

The potential impacts of CO₂-induced climate change on terrestrial carbon storage was estimated using the Holdridge Life-Zone Classification and four climate change scenarios derived from general circulation models. Carbon values were assigned to life-zones and their associated soils from published studies. All four scenarios suggest an increase in area occupied by forests although details of predicted patterns vary among the scenarios. There is a poleward shift of the forested zones, with an increase in the areal extent of tropical forests and a shift of the boreal forest zone into the region currently occupied by tundra. Terrestrial carbon storage increased from 0.4% (8.5 Gt) to 9.5% (180.5 Gt) above estimates for present conditions. These changes represent a potential reduction of 4 to 85 ppm on elevated atmospheric CO₂ levels.

KEYWORDS: CO₂, INCREASE

2241

Smith, W.K., and R.A. Donahue. 1991. Simulated influence of altitude on photosynthetic CO₂ uptake potential in plants. *Plant, Cell and Environment* 14(1):133-136.

A simulation of the quantitative influence of altitude on photosynthetic CO₂ uptake capability (A(P)) included the effects of predicted changes (1) in air temperature (lapse rate) and (2) leaf temperature, (3) ambient pressure and CO₂ concentration, and (4) the diffusion coefficient for CO₂ in air. When a dry lapse rate (0.01-degrees-C m⁻¹) in air temperature was simulated, significant declines (up to 14%) in A(P) were predicted from sea level to 4km altitude. A moist lapse rate of 0.003-degrees-C m⁻¹ resulted in less than a 4% decrease in A(P) over the same altitude range. When natural leaf temperatures (predicted from heat balance analyses) were simulated, A(P) was significantly greater (almost-equal-to 20%) than when leaf temperatures were considered equal to air temperature for all lapse conditions. There was virtually no change in A(P) with altitude when predicted leaf temperatures and moist lapse conditions were simulated. There was a significant (almost-equal-to 10%) increase in A(P) with altitude when leaf temperature was held constant at 30-degrees- C (regardless of altitude) under moist lapse conditions. Future studies evaluating the effects of elevation on photosynthesis could benefit from the above considerations of the effects of natural leaf temperature regimes and prevailing lapse conditions on CO₂ uptake potential.

KEYWORDS: CONDUCTANCE, LEAF ANATOMY

2242

Socias, F.X., H. Medrano, and T.D. Sharkey. 1993. Feedback limitation of photosynthesis of *Phaseolus-vulgaris* L grown in elevated CO₂. *Plant, Cell and Environment* 16(1):81-86.

The capacity for photosynthesis is often affected when plants are grown in air with elevated CO₂ partial pressure. We grew *Phaseolus vulgaris* L. in 35 and 65Pa CO₂ and measured photosynthetic parameters. When assayed at the growth CO₂ level, photosynthesis was equal in the two CO₂ treatments. The maximum rate of ribulose-1,5-bisphosphate (RuBP) consumption was lower in plants grown at 65Pa, but the CO₂ partial pressure at which the maximum occurred was higher in the high-CO₂-grown plants, indicating acclimation to high CO₂. The acclimation of RuBP consumption to CO₂ involved a reduction of the activity of RuBP carboxylase which resulted from reduced carbamylation, not a loss of protein. The rate of RuBP consumption declined with CO₂ when the CO₂ partial pressure was above 50Pa in plants grown under both CO₂ levels. This was caused by feedback inhibition as judged by a lack of response to removing O₂ from the air stream. The rate of photosynthesis at high CO₂ was lower in the high-CO₂-grown plants and this was correlated with reduced activity of sucrose-phosphate synthase. This is only the second report Of O₂-insensitive

photosynthesis under growth conditions for plants grown in high CO₂.

KEYWORDS: ACCLIMATION, CARBON DIOXIDE, GAS-EXCHANGE, ISOPRENE EMISSION, LEAVES, PHOTORESPIRATION, PLANTS, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, RUBISCO, SUCROSE PHOSPHATE SYNTHASE

2243

Solarova, J., and J. Pospisilova. 1997. Effect of carbon dioxide enrichment during in vitro cultivation and acclimation to ex vitro conditions. *Biologia Plantarum* 39(1):23-30.

Tobacco and carnation plantlets were grown in vitro on Murashige and Skoog's medium with 2% saccharose. Carnation plantlets were also grown fully photoautotrophically on a medium without saccharose. The ambient CO₂ concentration was increased from 0.6 to 10 or 40 g m⁻³ during the last 3 weeks of in vitro cultivation or during the first 3 weeks of acclimation to ex vitro condition (plantlets transplanted to pots with sand and nutrient solution) or during both growth phases. CO₂ enrichment during in vitro cultivation markedly stimulated growth of tobacco plantlets, and also of carnation plantlets, both with and without saccharose. CO₂ enrichment during the acclimation period promoted plant growth more effectively in plantlets grown in vitro at a CO₂ concentration of 0.6 g m⁻³ than in plantlets grown in either growth phase at higher CO₂ concentrations.

KEYWORDS: CO₂- ENRICHMENT, GROWTH, INVITRO, PHOTOSYNTHESIS, PLANTLETS, RASPBERRY, STRAWBERRY

2244

Sombroek, W.G., F.O. Nachtergaele, and A. Hebel. 1993. Amounts, dynamics and sequestering of carbon in tropical and subtropical soils. *Ambio* 22(7):417-426.

The organic carbon pool in the upper 1 m of the world's soils contains 1220 Gt organic carbon, 1.5 times the total for the standing biomass. In the widespread deep soils in the tropics the carbon stored below 1 m may add about 50 Gt C. The contributions of charcoal, roots and soil fauna should be added to these totals. The much less dynamic carbonate-carbon pool amounts to 720 Gt C. Changes in land use, particularly by clearing of forests, reduce organic carbon by 20 to 50% in the upper soil layers, but little in deeper layers. On the other hand, there are indications that a human-induced enrichment of soil organic matter can be maintained over centuries. Research on the causative soil processes should be supported, because an improved understanding of this phenomenon might lead to better management strategies and sound programs to stimulate organic carbon storage and fertility levels in tropical and subtropical soils. Recent research data on the CO₂ fertilization effect and the associated antitranspiration effect due to an increase of CO₂ in the atmosphere indicate that a positive influence on soil organic carbon levels can be expected.

KEYWORDS: AMAZON, BIOMASS, BIOSPHERE, CYCLE, FORESTS, STORAGE

2245

Sommerfeld, R.A., W.J. Massman, R.C. Musselman, and A.R. Mosier. 1996. Diffusional flux of CO₂ through snow: Spatial and temporal variability among alpine-subalpine sites. *Global Biogeochemical Cycles* 10(3):473-482.

Three alpine and three subalpine sites were monitored for up to 4 years to acquire data on the temporal and spatial variability of CO₂ flux through snowpacks. We conclude that the snow formed a passive cap which controlled the concentration of CO₂ at the snow-soil interface,

while the flux of CO₂ into the atmosphere was controlled by CO₂ production in the soil. Seasonal variability in the flux at all sites was characterized by early winter minima followed by a rise in flux that averaged 70% above the minima over about a 1-month period. The seasonal variability was not related to soil temperatures which remained relatively constant. Interannual variability was small, and spatial variability was smaller than previously reported. Spatial variability on a scale of 1 to 10 m was less than 30% of the average fluxes and not significantly greater than estimated error in most cases. Spatial variability on a scale of 10- to 100-m was about a factor of 2 and on a scale of 100 to 1000 m was about a factor of 4. The 100- to 1000-m variability was complicated by the fact that the sites were in different ecosystems, alpine and subalpine, and at different elevations. We attribute the small variability at the 1- to 10- m scale to the deep snow cover, from 1.4 to 5 m. We hypothesize that horizontal diffusion under the snow cover reduced small- scale horizontal gradients, while the insulating effect of the deep snow cover kept the soil temperature and moisture relatively constant. Equivalent annual wintertime flux averaged about 95 g C m⁻² yr⁻¹ in the alpine and about 232 g C m⁻² yr⁻¹ in the subalpine sites. Measurements of CO₂ concentrations at 0.2 and 0.5 m in the soil of one of the subalpine sites indicated that production early in the snow season occurred at or below 0.5 m while production between 0.5 m, and the surface became important after the start of the melt season.

KEYWORDS: SOILS

2246

Sonesson, M., T.V. Callaghan, and L.O. Bjorn. 1995. Short-term effects of enhanced UV-B and CO₂ on lichens at different latitudes. *Lichenologist* 27:547-557.

Interaction effects of UV-B and CO₂ on three lichens species, *Cladonia arbuscula*, *Cetraria islandica* and *Stereocaulon paschale*, from two latitudinal sites, 68 degrees N and 56 degrees N, were studied in a laboratory experiment. The response of the plants was recorded by measuring their chlorophyll fluorescence. All species had a similar response to enhanced UV-B depending on the latitude from which the population came and the time of the season when they were sampled. Overall, there was a significant increase in photosystem II yield (as measured by a fluorescence technique) due to UV-B and no separate effect due to enhanced CO₂, although there was a significant interaction between CO₂ and UV-B. The increase due to UV-B was at the low CO₂ level. There were also significant differences in response due to latitude. The results contradict our hypotheses that negative effects of UV-B would be larger in the North than in the South and that a negative response should be especially large during the early season. (C) 1995 The British Lichen Society

KEYWORDS: ALPINE LIFE ZONE, BLUE-GREEN PHYCOBIONTS, CARBON DIOXIDE, CHLOROPHYLL FLUORESCENCE, GROWTH, MARINE DIATOMS, PHOTOSYNTHETIC CHARACTERISTICS, PLANTS, RADIATION, STRATOSPHERIC OZONE

2247

Sonesson, M., T.V. Callaghan, and B.A. Carlsson. 1996. Effects of enhanced ultraviolet radiation and carbon dioxide concentration on the moss *Hylocomium splendens*. *Global Change Biology* 2(1):67-73.

In a laboratory experiment interaction effects of UV-B and CO₂ on photosynthesis and growth of the moss *Hylocomium splendens* were studied. The plants were exposed to two CO₂ levels (350 ppm and 600 ppm) and three UV-B levels (no UV-B, ambient UV-B and that corresponding to 20% ozone depletion) for 5 months. The effects were recorded by measuring the photosynthetic response and growth of the plants. There was a statistically significant change in photosynthetic

efficiency and maximum photosynthetic rates due to time and to enhanced CO₂ concentration, whereas there was no effect due to UV-B. There was a decreased growth due to both UV-B and CO₂ and an interaction effect on growth (in length). The UV-B dose corresponding to the ambient level had a larger reducing effect on growth than the highest UV-B dose. This was a counter-intuitive result and the following tentative interpretation was made: differences in the measured UV-A/UV-B/PAR ratios between the treatments could explain the result provided there was a non-linear response to UV over the range of irradiance levels used.

KEYWORDS: ACTION SPECTRUM, CO₂, DAMAGE, GROWTH, IRRADIATION, LIGHT, MARINE DIATOMS, PHOTOSYNTHETIC CHARACTERISTICS, PLANTS, UV-B RADIATION

2248

Soule, P.T., and P.A. Knapp. 1999. Western juniper expansion on adjacent disturbed and near-relict sites. *Journal of Range Management* 52(5):525-533.

We determined rates of western juniper (*Juniperus occidentalis* spp. *occidentalis* Hook.) density and cover change during the period 1951 to 1994 at 3 adjacent sites with nearly identical elevation, slope, aspect, soils, plant communities, and climate, but different land-use histories. The 3 sites are located in central Oregon at the confluence of the Deschutes and Crooked Rivers. Two of the sites are typical of central Oregon rangelands in that they have a history of anthropogenic disturbance including active fire suppression and domestic livestock grazing. The third site is a relict mesa that is a protected Research Natural Area and has experienced minimal anthropogenic impacts. We used large scale aerial photography to determine cover and density of western juniper in 1951, 1956, 1961, 1972, 1982, and 1994. We found that western juniper density and cover during the last 4 decades increased at all sites, with changes on the relict site similar to those on one of the disturbed sites. We suggest that even though 2 of the traditionally cited causes of western juniper expansion since the late 1800s (altered fire regimes, domestic livestock grazing) may have contributed to expansion on our disturbed sites, these mechanisms can not explain expansion on the near-relict mesa. Further, we examined climatic changes since 1900 in the region and concluded that the data did not fully support a climate-driven mechanism for the expansion. In seeking to explain western juniper expansion on semiarid rangelands, we suggest that all potential causal mechanisms (e.g., fire history, biological inertia, climate, domestic grazing, atmospheric CO₂ enrichment) be considered.

KEYWORDS: ATMOSPHERIC CO₂ ENRICHMENT, CARBON DIOXIDE, CENTRAL OREGON, GROWTH, OCCIDENTALIS, TRENDS, UNITED-STATES, VEGETATION CHANGE

2249

Soussana, J.F., E. Casella, and P. Loiseau. 1996. Long-term effects of CO₂ enrichment and temperature increase on a temperate grass sward .2. Plant nitrogen budgets and root fraction. *Plant and Soil* 182(1):101-114.

Perennial ryegrass swards were grown in large containers on a soil and were exposed during two years to elevated (700 μ mol L⁻¹) or ambient atmospheric CO₂ concentration at outdoor temperature and to a 3 degrees C increase in air temperature in elevated CO₂. The nitrogen nutrition of the grass sward was studied at two sub-optimal (160 and 530 kg N ha⁻¹ y⁻¹) and one non-limiting (1000 kg N ha⁻¹ y⁻¹) N fertilizer supplies. At cutting date, elevated CO₂ reduced by 25 to 33%, on average, the leaf N concentration per unit mass. Due to an increase in the leaf blade weight per unit area in elevated CO₂, this decline did not translate for all cuts in a lower N concentration per unit leaf blade

area. With the non-limiting N fertilizer supply, the leaf N concentration (% N) declined with the shoot dry-matter (DM) according to highly significant power models in ambient (% N=4.9 DM^{-0.38}) and in elevated (% N=5.3 DM^{-0.52}) CO₂. The difference between both regressions was significant and indicated a lower critical leaf N concentration in elevated than in ambient CO₂ for high, but not for low values of shoot biomass. With the sub-optimal N fertilizer supplies, the nitrogen nutrition index of the grass sward, calculated as the ratio of the actual to the critical leaf N concentration, was significantly lowered in elevated CO₂. This indicated a lower inorganic N availability for the grass plants in elevated CO₂, which was also apparent from the significant declines in the annual nitrogen yield of the grass sward and in the nitrate leaching during winter. For most cuts, the harvested fraction of the plant dry-matter decreased in elevated CO₂ due, on average, to a 45-52% increase in the root phytomass. In the same way, a smaller share of the plant total nitrogen was harvested by cutting, due, on average, to a 25-41% increase in the N content of roots. The annual means of the DM and N harvest indices were highly correlated to the annual means of the nitrogen nutrition index. Changes in the harvest index and in the nitrogen nutrition index between ambient and elevated CO₂ were also positively correlated. The possible implication of changes in the soil nitrogen cycle and of a limitation in the shoot growth potential of the grass in elevated CO₂ is discussed.

KEYWORDS: CANOPY, CARBON-DIOXIDE CONCENTRATION, DRY-MATTER, ELEVATED CO₂, GROWTH, LEAF, NUTRITION, PERENNIAL RYEGRASS, PHOTOSYNTHESIS, TALL FESCUE

2250

Soussana, J.F., and U.A. Hartwig. 1996. The effects of elevated CO₂ on symbiotic N-2 fixation: A link between the carbon and nitrogen cycles in grassland ecosystems. *Plant and Soil* 187(2):321-332.

The response of plants to elevated CO₂ is dependent on the availability of nutrients, especially nitrogen. It is generally accepted that an increase in the atmospheric CO₂ concentration increases the C:N ratio of plant residues and exudates. This promotes temporary N-immobilization which might, in turn, reduce the availability of soil nitrogen. In addition, both a CO₂ stimulated increase in plant growth (thus requiring more nitrogen) and an increased N demand for the decomposition of soil residues with a large C:N will result under elevated CO₂ in a larger N-sink of the whole grassland ecosystem. One way to maintain the balance between the C and N cycles in elevated CO₂ would be to increase N-input to the grassland ecosystem through symbiotic N-2 fixation. Whether this might happen in the context of temperate ecosystems is discussed, by assessing the following hypothesis: i) symbiotic N-2 fixation in legumes will be enhanced under elevated CO₂, ii) this enhancement of N-2 fixation will result in a larger N-input to the grassland ecosystem, and iii) a larger N input will allow the sequestration of additional carbon, either above or below-ground, into the ecosystem. Data from long-term experiments with model grassland ecosystems, consisting of monocultures or mixtures of perennial ryegrass and white clover, grown under elevated CO₂ under free-air or field-like conditions, supports the first two hypothesis, since: i) both the percentage and the amount of fixed N increases in white clover grown under elevated CO₂ ii) the contribution of fixed N to the nitrogen nutrition of the mixed grass also increases in elevated CO₂. Concerning the third hypothesis? an increased nitrogen input to the grassland ecosystem from N-2 fixation usually promotes shoot growth (above-ground C storage) in elevated CO₂. However, the consequences of this larger N input under elevated CO₂ on the belowground carbon fluxes are not fully understood. On one hand, the positive effect of elevated CO₂ on the quantity of plant residues might be overwhelming and lead to an increased long-term below-ground C storage; on the other hand, the enhancement of the decomposition process by the N-rich legume material might favour carbon turn-over and, hence, limit the storage of below-ground carbon.

KEYWORDS: ACETYLENE-REDUCTION ACTIVITY, ATMOSPHERIC CO₂, BIRD'S-FOOT-TREFOIL, CLOVER TRIFOLIUM-REPENS, HYDROGEN EVOLUTION, LEGUME NODULES, MEDICAGO-SATIVA, NITRATE INHIBITION, ROOT NODULE ACTIVITY, WHITE CLOVER

2251

Sozzi, G.O., G.D. Trinchero, and A.A. Frascina. 1999. Controlled-atmosphere storage of tomato fruit: low oxygen or elevated carbon dioxide levels alter galactosidase activity and inhibit exogenous ethylene action. *Journal of the Science of Food and Agriculture* 79(8):1065-1070.

The effects of 3% O₂ and 20% CO₂, both alone and together with 100 $\mu\text{g g}^{-1}$ C₂H₄, on ethylene production, chlorophyll degradation, carotenoid biosynthesis and α - and β -galactosidase activity in breaker tomato (*Lycopersicon esculentum* Mill) fruit were investigated. The low O₂ and high CO₂ atmospheres prevented the rise in ethylene production, total carotenoid and lycopene biosynthesis and α - and β -galactosidase activity and slowed down chlorophyll degradation and loss of firmness ($P < 0.05$). These suppressive effects were not reversed, or only in part - in the case of chlorophyll breakdown - by addition of 100 $\mu\text{g g}^{-1}$ C₂H₄ to said controlled atmospheres. After transfer from the various atmospheres to air, flesh firmness decreased and ethylene production, total carotenoids, lycopene and β -galactosidase activity increased but these parameters were, in all cases, still significantly different from those of fruit held in air. Keeping tomatoes in controlled atmospheres, even in the presence of ethylene, had marked residual effects. Results suggest an antagonism between elevated CO₂/low O₂ and exogenous ethylene which could determine most of the ripening parameter behaviour under controlled-atmosphere storage, though a direct regulatory mechanism by O₂ and/or CO₂ should not be discarded. (C) 1999 Society of Chemical Industry.

KEYWORDS: BIOSYNTHESIS, CELL-WALL POLYSACCHARIDES, CELLULOSE, DEGRADATION, POLYGALACTURONASE, PROTEIN, RNA, STRESS

2252

Spring, G.M., G.H. Priestman, and J.P. Grime. 1996. A new field technique for elevating carbon dioxide levels in climate change experiments. *Functional Ecology* 10(4):541-545.

1. A compact, low-cost, free-air carbon dioxide enrichment system for use in climate change experiments is described. The system has been used in a small-scale study of the effects of an enriched carbon dioxide atmosphere on the growth and functioning of a natural plant community. 2. The experiment ran for 4 months in summer on a nutrient-poor limestone grassland in Derbyshire. The study examined the separate and combined effects of elevated CO₂, temperature and soil nutrient status on the growth of seedlings of obligate mycorrhizal and non-mycorrhizal plant species native to the site. 3. It was demonstrated that the CO₂ elevation could be controlled within the limits set for 64% of the time. Significant effects of elevated CO₂ on the growth and recruitment of seedlings were found in the presence of added nutrients and elevated temperatures.

KEYWORDS: CO₂-ENRICHMENT, GROWTH, LIGHT, NUTRIENTS, PLANTS, RESPONSES

2253

Spunda, V., J. Kalina, M. Cajanek, H. Pavlickova, and M.V. Marek. 1998. Long-term exposure of Norway spruce to elevated CO₂ concentration induces changes in photosystem II mimicking an adaptation to increased irradiance. *Journal of Plant Physiology* 152(4-5):413-419.

Fifteen-year-old Norway spruces (*Picea abies* [L.] Karst.) were grown in open top chambers (OTC) at ambient (A) and elevated (i.e. ambient + 350 $\mu\text{mol}(\text{CO}_2)\text{mol}^{-1}$) concentrations of CO₂ (E) for four growing seasons (1992-1995). During this time period several examples of the depression of photosynthetic activities were observed for E needles. In order to better characterize the nature of this depression the gas exchange and fluorescence parameters were analyzed on current year needles during the last season (July 1995). The photon flux density response curves of CO₂ uptake (P-N) revealed a significantly reduced stimulation of P-N for E needles as compared with short-term exposure to doubled CO₂. Moreover, the sudden exposure of E shoots to 350 $\mu\text{mol}(\text{CO}_2)\text{mol}^{-1}$ at saturating irradiance revealed a depression of both P-N_{max} (by 20 %) and quantum yield of PS II (by 32 %) compared with A shoots measured at 350 $\mu\text{mol}(\text{CO}_2)\text{mol}^{-1}$. The data supporting the diminished light harvesting system of photosystem II (PS II) in E shoots compared with A shoots were obtained from pigment analysis, low temperature fluorescence spectra and Chl *a* fluorescence induction kinetics. The relative proportion of inactive reaction centres of PS II determined from F-pl of the fluorescence induction was 20 % higher for E needles. These changes found for E needles mimicked an adaptation of PS II to increased irradiance compared with A needles. As the irradiance exposure was the same for the examined needles from both E and A spruces we suggest that these changes reported for E needles resulted from the feed-back limitation of photochemical reactions due to suppressed electron transport through the plastoquinone pool.

KEYWORDS: ACCLIMATION, ATMOSPHERIC CO₂, CARBON DIOXIDE, CHLOROPHYLL FLUORESCENCE, GAS-EXCHANGE, GROWTH, LEAVES, PHOTONHIBITION, PHOTOSYNTHESIS, TOMATO PLANTS

2254

Sritharan, R., H. Caspari, and F. Lenz. 1992. Influence of CO₂ enrichment and phosphorus supply on growth, carbohydrates and nitrate utilization of kohlrabi plants. *Gartenbauwissenschaft* 57(5):246-251.

Kohlrabi (*Brassica oleracea* var. *gongylodes* (L.) cv. Express Forcer) plants were grown in sand with adequate nutrient supply. From two weeks after germination until harvest they were treated with two levels of phosphorus supply (1.0 or 0.005 mM P). Four weeks after introducing the P supply regimes the plants were exposed to either a low (300 $\mu\text{L CO}_2 \text{ L}^{-1}$) or high (900 $\mu\text{L CO}_2 \text{ L}^{-1}$) CO₂ concentration in growth chambers for three weeks. At elevated CO₂ concentration plants with 1.0 mM phosphorus produced a larger leaf area and dry matter than those grown at low CO₂. At reduced P supply CO₂ enrichment promoted leaf senescence and did not increase growth and dry matter. Phosphorus deficiency resulted in increased accumulation of starch in leaves, tuber, and roots and reduced NO₃-N concentrations in all plant parts. The CO₂ enrichment reduced N and NO₃ concentration and increased nitrate utilization efficiency at both P levels. Phosphorus deficiency decreased nitrogen, potassium, calcium, and magnesium concentrations in leaves particularly at high CO₂.

KEYWORDS: ACCUMULATION, CARBON DIOXIDE, EXCHANGE, LEAVES, NITROGEN, NUTRITION, PHOSPHATE STATUS, PHOTOSYNTHESIS, REDUCTASE-ACTIVITY, STARCH

2255

Sritharan, R., and F. Lenz. 1992. Effects of carbon-dioxide enrichment and nitrogen supply on kohlrabi (*brassica-oleracea* var *gongylodes* L.) .1. Water-use, gas-exchange, and carbohydrate partitioning. *Gartenbauwissenschaft* 57(3):138-145.

Six weeks old kohlrabi plants (*Brassica oleracea* var. *gongylodes* [L.] cv.

Express Forcer) were grown in growth chambers for three weeks at two levels of CO₂ concentration (300- μ l CO₂ l⁻¹-low or 900- μ l CO₂ l⁻¹-high) and three levels of N-nutritional regimes (0.1, 1.0 or 6.0 mM nitrate supply). Carbon dioxide enrichment significantly increased total water uptake of plants at all N supply levels. Water use efficiency, photosynthesis and stomatal conductance were increased by high CO₂ only at 1.0 and 6.0 mM supply and reduced at the lowest N level. Photosynthetic efficiency (μ -Mol CO₂ fixed m⁻² s⁻¹ per μ -l intercellular CO₂ l⁻¹) was reduced by both low N supply and CO₂ enrichment. Intercellular CO₂ concentration was not affected by N deficiency at both CO₂ levels. Low NO₃ had a lesser effect on photosynthesis than on leaf area growth; photosynthetic rates of mature leaves at both CO₂ levels were lowered by about 30 % as compared to the respective controls, after seven weeks of reduction in NO₃ supply. In leaves lowest NO₃ treatment increased starch and sucrose and in roots starch glucose, fructose, and sucrose and in tuber starch concentrations. Photosynthetic reduction at low N supply showed a significant correlation with leaf starch concentration at both CO₂ levels indicating that the inhibition is a result of feed back inhibition. Carbohydrate partitioning within the plant organs were predominantly governed by N supply levels than CO₂ treatments.

KEYWORDS: ACCUMULATION, CO₂, CONDUCTANCE, COTTON, LEAVES, PHOTOSYNTHESIS, STRESS, TRANSPIRATION

2256

Staddon, P.L. 1998. Insights into mycorrhizal colonisation at elevated CO₂: a simple carbon partitioning model. *Plant and Soil* 205(2):171-180.

A simulation model was used to investigate the effect of an increased rate of plant photosynthesis at enhanced atmospheric CO₂ concentration on a non-leguminous plant-mycorrhizal fungus association. The model allowed the user to modify carbon allocation patterns at three levels: (1) within the plant (shoot-root), (2) between the plant and the mycorrhizal fungus and (3) within the mycorrhizal fungus (intraradical- extraradical structures). Belowground (root and fungus) carbon losses via respiration (and turnover) could also be manipulated. The specific objectives were to investigate the dynamic nature of the potential effects of elevated CO₂ on mycorrhizal colonisation and to elucidate some of the various mechanisms by which these effects may be negated. Many of the simulations showed that time (i.e. plant age) had a more significant effect on the observed stimulation of mycorrhizal colonisation by elevated CO₂ than changes in carbon allocation patterns or belowground carbon losses. There were two main mechanisms which negated a stimulatory effect of elevated CO₂ on internal mycorrhizal colonisation: an increased mycorrhizal carbon allocation to the external hyphal network and an increased rate of mycorrhizal respiration. The results are discussed in relation to real experiments. The need for studies consisting of multiple harvests is emphasised, as is the use of allometric analysis. Implications at the ecosystem level are discussed and key areas for future research are presented.

KEYWORDS: ATMOSPHERIC CO₂, BOUTELOUA-GRACILIS, CLIMATE CHANGE, DIOXIDE, GROWTH, INFECTION UNITS, PLANTS, RESPONSES, ROOTS, TRIFOLIUM-SUBTERRANEUM L

2257

Staddon, P.L., and A.H. Fitter. 1998. Does elevated atmospheric carbon dioxide affect arbuscular mycorrhizas? *Trends in Ecology and Evolution* 13(11):455-458.

It is well established that an increase in the concentration of atmospheric CO₂ stimulates plant growth. Recently, many researchers have concluded that elevated CO₂ concentrations also stimulate mycorrhizal colonization. However, new evidence suggests that the observed CO₂

effects on arbuscular mycorrhizal fungi are indirect and are a result of faster plant growth at higher CO₂ concentrations. Potential changes to species assemblages of mycorrhizal fungi could affect soil carbon storage and, consequently, the feedback effects of terrestrial soil-vegetation systems on global environmental change.

KEYWORDS: BOUTELOUA-GRACILIS, CO₂- ENRICHMENT, COLONIZATION, GROWTH, INFECTION, QUERCUS-ALBA, RESPONSES, ROOT, SEEDLINGS, SOIL

2258

Staddon, P.L., A.H. Fitter, and J.D. Graves. 1999. Effect of elevated atmospheric CO₂ on mycorrhizal colonization, external mycorrhizal hyphal production and phosphorus inflow in *Plantago lanceolata* and *Trifolium repens* in association with the arbuscular mycorrhizal fungus *Glomus mosseae*. *Global Change Biology* 5(3):347-358.

Plantago lanceolata and *Trifolium repens* were grown under ambient (400 μ mol mol⁻¹) and elevated (650 μ mol mol⁻¹) atmospheric CO₂ conditions. Plants were inoculated with the arbuscular mycorrhizal fungus *Glomus mosseae* and given a phosphorus supply in the form of bonemeal. Six sequential harvests were taken in order to determine whether the effect of elevated CO₂ on internal mycorrhizal colonization and external hyphal production was independent of the stimulatory effect of elevated CO₂ on plant growth. At a given time, elevated CO₂ increased the percentage of root length colonized (RLC), the total length of colonized root and the external mycorrhizal hyphal (EMH) density and decreased the ratio of EMH to total length of colonized root. When plant size was taken into account, the CO₂ effect on RLC and total length of colonized root was greatly reduced and only apparent for early harvests in *T. repens*) and the effects on the EMH parameters disappeared. Root tissue P concentration was unchanged at elevated CO₂, but there was a decrease in shoot P at the later harvests. There was no direct effect of elevated CO₂ on P inflow for the earlier period (< 50 d) of the experiment. However, over the last period, there was a significant negative effect of elevated CO₂ on P inflow for both species, independent of plant size. It is concluded that elevated CO₂ had no direct effect on mycorrhizal colonization or external hyphal production, and that any observed effects on a time basis were due to faster growing plants at elevated CO₂. However, for older plants, elevated CO₂ had a direct negative effect on P inflow. This decrease in P inflow coincides with the observed decrease in shoot P concentration. This is discussed in terms of downregulation of photosynthesis often seen in elevated CO₂ grown plants, and the potential for mycorrhizas (via external hyphal turnover) to alleviate the phenomenon. The direction for future research is highlighted, especially in relation to carbon flow to and storage in the soil.

KEYWORDS: BOUTELOUA-GRACILIS, CLIMATE CHANGE, ENRICHMENT, GLOBAL CARBON-CYCLE, GROWTH, QUERCUS-ALBA, ROOT, SINK ACTIVITY, SOIL, SUBTERRANEUM L

2259

Staddon, P.L., A.H. Fitter, and D. Robinson. 1999. Effects of mycorrhizal colonization and elevated atmospheric carbon dioxide on carbon fixation and below-ground carbon partitioning in *Plantago lanceolata*. *Journal of Experimental Botany* 50(335):853-860.

Plantago lanceolata with or without the mycorrhizal fungus *Glomus mosseae* were grown over a 100 d period under ambient (380 \pm 50 μ mol mol⁻¹) and elevated (600 \pm 150 μ mol mol⁻¹) atmospheric CO₂ conditions. To achieve similar growth, non-mycorrhizal plants received phosphorus in solution whereas mycorrhizal plants were supplied with bonemeal. Measures of plant growth, photosynthesis and carbon input to the soil were obtained. Elevated CO₂ stimulated plant growth to the same extent in mycorrhizal and non-mycorrhizal plants,

but had no effect on the partitioning of carbon between shoots and roots or on shoot tissue phosphorus concentration. Mycorrhizal colonization was low, but unaffected by CO₂ treatment. Net photosynthesis was stimulated both by mycorrhizal colonization and elevated CO₂, and there was a more than additive effect of the two treatments on net photosynthesis. Colonization by mycorrhizal fungi inhibited acclimation, in terms of net carbon assimilation, of plants to elevated CO₂. C-13 natural abundance techniques were used to measure carbon input into the soil, although the results were not conclusive. Direct measurements of below-ground root biomass showed that elevated CO₂ did stimulate carbon flow below-ground and this was higher in mycorrhizal than non-mycorrhizal plants. For the four treatment combinations, the observed relative differences in amount of below-ground carbon were compared with those expected from the differences in net photosynthesis. A considerable amount of the extra carbon fixed both as a result of mycorrhizal colonization and growth in elevated CO₂ did not reveal itself as increased plant biomass. As there was no evidence for a substantial increase in soil organic matter, most of this extra carbon must have been respired by the mycorrhizal fungus and the roots or by the plants as dark-respiration. The need for detailed studies in this area is emphasized.

KEYWORDS: CO₂-ENRICHMENT, GLOMUS-MOSSEAE, GROWTH, NATURAL ECOSYSTEMS, PHOTOSYNTHESIS, RESPONSES, SOIL, SOURCE-SINK RELATIONS, TRIFOLIUM-REPENS, USE EFFICIENCY

2260

Staddon, P.L., J.D. Graves, and A.H. Fitter. 1998. Effect of enhanced atmospheric CO₂ on mycorrhizal colonization by *Glomus mosseae* in *Plantago lanceolata* and *Trifolium repens*. *New Phytologist* 139(3):571-580.

Plantago lanceolata L. and *Trifolium repens* L. were grown for 16 wk in ambient (360 $\mu\text{mol mol}^{-1}$) and elevated (610 $\mu\text{mol mol}^{-1}$) atmospheric CO₂. Plants were inoculated with the arbuscular mycorrhizal (AM) fungus *Glomus mosseae* (Nicol. & Gerd.) Gerdemann & Trappe and given a phosphorus supply in the form of bonemeal, which would not be immediately available to the plants. Seven sequential harvests were taken to determine whether the effect of elevated CO₂ on mycorrhizal colonization was independent of the effect of CO₂ on plant growth. Plant growth analysis showed that both species grew faster in elevated CO₂ and that *P. lanceolata* had increased carbon allocation towards the roots. Elevated CO₂ did not affect the percentage of root length colonized (RLC); although total colonized root length was greater, when plant size was taken into account this effect disappeared. This finding was also true for root length colonized by arbuscules. No CO₂ effect was found on hyphal density (colonization intensity) in roots. The P content of plants was increased at elevated CO₂, although both shoot and root tissue P concentration were unchanged. This was again as a result of bigger plants at elevated CO₂. Phosphorus inflow was unaffected by CO₂ concentrations. It is concluded that there is no direct permanent effect of elevated CO₂ on mycorrhizal functioning, as internal mycorrhizal development and the mycorrhizal P uptake mechanism are unaffected. The importance of sequential harvests in experiments is discussed. The direction for future research is highlighted, especially in relation to C storage in the soil.

KEYWORDS: BOUTELOUA-GRACILIS, CLIMATE CHANGE, ELEVATED CO₂, ENRICHMENT, GLOBAL CARBON-CYCLE, GROWTH, QUERCUS-ALBA, RESPONSES, ROOTS, SINK

2261

Staddon, P.L., J.D. Graves, and A.H. Fitter. 1999. Effect of enhanced atmospheric CO₂ on mycorrhizal colonization and phosphorus inflow in 10 herbaceous species of contrasting growth strategies. *Functional*

Ecology 13(2):190-199.

1. Ten herbaceous species were grown over a 4-month period under ambient (360 $\mu\text{mol mol}^{-1}$) and elevated (610 $\mu\text{mol mol}^{-1}$) atmospheric CO₂ conditions. Plants were inoculated with the arbuscular mycorrhizal (AM) fungus *Glomus mosseae* and given a phosphorus (P) supply which was not immediately available to the plants. 2. Multiple harvests were taken in order to determine whether the effect of elevated CO₂ on mycorrhizal colonization and phosphorus inflow was independent of its effect on plant growth. 3. All species grew faster under elevated CO₂ and carbon partitioning was altered, generally in favour of the shoots. All species responded similarly to elevated CO₂. 4. Elevated CO₂ did not affect the percentage of root length colonized by AM fungi, but the total amount of colonized root length was increased, because the plants were bigger. 5. Elevated CO₂ increased total P content, but had little or no effect on P concentration. At a given age, P inflow was stimulated by elevated CO₂, but when root length was taken into account the CO₂ effect disappeared. 6. In these host species there is no evidence for a direct effect of elevated CO₂ on mycorrhizal functioning, because both internal mycorrhizal colonization and P inflow are unaffected. 7. Future research should concentrate on the potential for carbon flow to the soil via the external mycelial network.

KEYWORDS: BOUTELOUA-GRACILIS, CLIMATE CHANGE, ELEVATED CARBON-DIOXIDE, ENRICHMENT, NUTRITION, PLANTAGO-LANCEOLATA, QUERCUS-ALBA, RESPONSES, ROOT, TRIFOLIUM-REPENS

2262

Stange, G. 1997. Effects of changes in atmospheric carbon dioxide on the location of hosts by the moth, *Cactoblastis cactorum*. *Oecologia* 110(4):539-545.

Sensory organs that detect CO₂ are common in herbivorous moths and butterflies, but their function has been unclear until now. As the CO₂ gradients in the vicinity of a host plant depend on its physiological condition, CO₂ could provide a sensory cue for the suitability of the plant as a larval food source. This study investigated whether changing the atmospheric CO₂ concentration affected oviposition by *Cactoblastis cactorum* on its host, the cactus *Opuntia stricta*. On host plants exposed to rapid fluctuations in CO₂ concentration, the frequency of oviposition was reduced by a factor of 3.2 compared to the control. As the fluctuations mask the much smaller CO₂ signals generated by the plants, this suggests that those signals constitute an important component of the host identification process. On host plants exposed to a constant background of doubled CO₂, oviposition was also reduced, by a factor of 1.8. An increased background reduces host signal detectability, partially as a consequence of a general principle of sensory physiology (Weber-Fechner's law), and partially due to other factors specific to CO₂-receptor neurons.

KEYWORDS: AUSTRALIA, BIOLOGICAL-CONTROL, ELEVATED CO₂, LEPIDOPTERA, NOCTUIDAE, OPEN-TOP CHAMBERS, OPUNTIA-STRICTA, PIT ORGAN, RECEPTORS, SELECTION

2263

Stanghellini, C., and J.A. Bunce. 1993. Response of photosynthesis and conductance to light, CO₂, temperature and humidity in tomato plants acclimated to ambient and elevated CO₂. *Photosynthetica* 29(4):487-497.

In tomato (*Lycopersicon esculentum* L.) plants, net carbon dioxide exchange rate (P(N)) response curves to both irradiance (I) and short-term [CO₂] were similar for plants grown at both 350 and 700 $\mu\text{mol CO}_2 \text{ m}^{-3}$. However, water vapor conductance (gH₂O) of plants grown at high [CO₂] was less sensitive to short term [CO₂] variations,

when measured at low vapor pressure difference, and was larger than the conductance of "ambient [CO₂]" plants when both were exposed to high [CO₂]. P(N) and g(H₂O) under high I increased with temperature over the range 18 to 32-degrees-C. P(N) of plants grown in both [CO₂] treatments increased at most about 25 % from 350 to 700 cm³ m⁻³ at 18 and 25-degrees-C, and decreased when exposed to 1000 cm³ m⁻³ at these temperatures. Thus increasing atmospheric [CO₂] might not increase P(N) by as much as expected and water use of crops might not decrease.

KEYWORDS: C-3, CARBON DIOXIDE, CARBOXYLASE, FIELD-GROWN TOMATO, HIGH ATMOSPHERIC CO₂, INHIBITION, O₂, SENSITIVITY, STOMATAL CLOSURE, TERM

2264

Steffen, W.L., W. Cramer, M. Plochl, and H. Bugmann. 1996. Global vegetation models: Incorporating transient changes to structure and composition. *Journal of Vegetation Science* 7(3):321-328.

We describe an approach for developing a Dynamic Global Vegetation Model (DGVM) that accounts for transient changes in vegetation distribution over a decadal time scale. The DGVM structure is based on a linkage between an equilibrium global vegetation model and smaller scale ecosystem dynamics modules that simulate the rate of vegetation change. Vegetation change is classified into four basic types, based largely on the projected change in above-ground biomass of the vegetation. These four types of change are: (1) dieback of forest, shrubland or grassland; (2) successional replacement within forest, shrubland or grassland; (3) invasion of forest, shrubland or grassland; (4) change in tree/grass ratio. We then propose an approach in which the appropriate ecosystem dynamics module for each type of change is applied and the grid cells of the global model updated accordingly. An approach for accounting for fire, as an example of a disturbance which may strongly influence the rate and spatial pattern of forest dieback, is incorporated. We also discuss data needs for the development, calibration and validation of the model.

KEYWORDS: ATMOSPHERE, CO₂, CO₂-INDUCED CLIMATE CHANGE, DEFORESTATION, ECOSYSTEMS, FORESTS, IMPACT, SIMULATION-MODEL, SOIL, TERRESTRIAL CARBON STORAGE

2265

Steffen, W.L., and J.S.I. Ingram. 1995. Global change and terrestrial ecosystems: An initial integration. *Journal of Biogeography* 22(2-3):165-174.

We present a framework for integrating GCTE's research programme based on three interacting axes-time, space and applicability. We use the contributed papers from the First GCTE Science Conference to undertake an initial integration of GCTE-type research using this three-axis structure. We assess where progress is being made, where progress is likely to be made in the near future, and where critical gaps exist which require a major effort to eliminate. Elevated CO₂ research is one of the most mature areas within GCTE, and provides scope for initial integration along all three axes. Soils, being key to the functioning of all terrestrial ecosystems, provide another excellent opportunity to integrate research along all three axes. A major obstacle to further integration is our lack of understanding of landscape-scale processes, particularly disturbances, and our ability to simulate global change impacts on them. GCTE's Focus 2, Change in Ecosystem Structure, is perhaps best placed to attack many of the gaps that prevent this further integration along space and time scales, and is now entering a rapid development phase; the other Foci also have a major role to play. Integration specifically along the applicability axis is being developed in some areas but requires an enhanced effort to achieve its potential to increase scientific efficiency and effectiveness. The emerging field of global ecology, i.e.

ecology at very large space and time scales, is progressing rapidly on the basis of linkages to more traditional ecological research at smaller scales, but requires further interaction with work along the applicability axis.

2266

Steinger, T., C. Lavigne, A. Birrer, K. Groppe, and B. Schmid. 1997. Genetic variation in response to elevated CO₂ in three grassland perennials - a field experiment with two competition regimes. *Acta Oecologica-International Journal of Ecology* 18(3):263-268.

Intraspecific Variation in the response to increased concentrations of atmospheric CO₂ was investigated in three plant species (*Bromus erectus*, *Prunella vulgaris*, *P. grandiflora*) in a calcareous grass land. Genotypes of each species were grown both in multispecies communities and under reduced competition pressure in tubes buried in the soil. Plant growth was reduced in the artificial communities but no significant effect of CO₂ was observed on any of the measured traits. Significant genotype by-CO₂ interactions were found in two species when plants were grown under reduced competition in the tubes. No genotype-by-CO₂ interactions were found for the same genotypes grown in the multispecies communities indicating that genetic variation was swamped by large environmental variation. Furthermore, no correlations were observed between CO₂ responses of identical genotypes grown individually in tubes and in multispecies communities. This result cautions about the ability to predict CO₂-induced evolutionary changes from data of individually-grown plants.

KEYWORDS: ENVIRONMENTS, PLANTS

2267

Stekiel, T.A., W.J. Stekiel, M. Tominaga, A. Stadnicka, Z.J. Bosnjak, and J.P. Kampine. 1996. Effect of halothane and isoflurane on in situ diameter responses of small mesenteric veins to acute graded hypercapnia. *Anesthesia and Analgesia* 82(2):349-357.

The purpose of the present study was to quantify the inhibitory effect of inhaled halothane and isoflurane on acute hypercapnia-induced responses of capacitance-regulating veins and related cardiovascular variables in response to sequential 40-s periods of 5%, 10%, 15%, and 20% inspired CO₂ (FICO₂). Measurements were made in normoxic alpha-chloralose- anesthetized rabbits before, during, and after either 0.75 minimum alveolar anesthetic concentration inhaled halothane or isoflurane. The graded hypercapnia caused graded venoconstriction and bradycardia but minimal pressor responses. Hypercapnia-induced venoconstriction was blocked by prior local superfusion of the exposed veins with 3 x 10⁻⁶ M tetrodotoxin. Both the hypercapnia-induced venoconstriction and bradycardia responses were significantly attenuated by halothane or isoflurane and did not fully recover after removal of the anesthetics from the circulation. Both anesthetics produced a significant baseline (i.e., prehypercapnia) hypotension and a tendency toward a resultant tachycardia. The baseline hypotension did not recover completely after elimination of the anesthetic. Neither anesthetic altered baseline vein diameter. These results agree with previous studies demonstrating that hypercapnic acidosis produces mesenteric venoconstriction by elevating excitatory sympathetic efferent neural input via activation of peripheral and central chemoreceptors and that bradycardia results from activation of compensatory baroreflexes. The neural components of these reflexes are possible primary sites for attenuation of these cardiovascular responses by halothane and isoflurane.

KEYWORDS: ANESTHESIA, ANESTHETIZED DOGS, BARORECEPTOR, CARBON DIOXIDE, CIRCULATION, HYPOXIC HYPERCAPNIA, RABBITS, REFLEX CONTROL, SYMPATHETIC-NERVE ACTIVITY, VASCULAR CAPACITANCE

2268

Sternberg, M., V.K. Brown, G.J. Masters, and I.P. Clarke. 1999. Plant community dynamics in a calcareous grassland under climate change manipulations. *Plant Ecology* 143(1):29-37.

This study investigates the effects of field manipulations of local climate to determine the potential impact of climate change on plant community dynamics in a calcareous grassland. The experimental site is located in a grassland at the Wytham estate, Oxfordshire, UK. The one hectare study area is within a 10 ha abandoned arable field on Jurassic corallian limestone. Two climate change scenarios were used: warmer winters with increased summer rainfall and warmer winters with summer drought. Plant cover and species richness were significantly increased in plots receiving supplemented summer rainfall, while the amount of litter was significantly reduced. Litter formation was significantly increased by winter warming and drought. The responses of the plant community to the climate manipulations were related to the life-history attributes of the dominant species. Seedling recruitment was limited by microsite availability, which also varied in the different climate manipulations. The results are discussed in terms of successional dynamics. They suggest that warmer winters may delay succession, as gap formation in the sward will provide sites for colonisation of annuals, thereby enabling their persistence in the sward. Under wetter conditions during summer, perennial grasses tend to close the sward, thereby inhibiting the establishment of later successional species.

KEYWORDS: ELEVATED CO₂, GROWTH, INSECT HERBIVORE INTERACTIONS, LITTER DECOMPOSITION, MECHANISMS, NITROGEN, RESPONSES, SEEDLING ESTABLISHMENT, TEMPERATURE, TUNDRA

2269

Stewart, J.D., and J. Hoddinott. 1993. Photosynthetic acclimation to elevated atmospheric carbon-dioxide and uv irradiation in pinus-banksiana. *Physiologia Plantarum* 88(3):493-500.

Pinus banksiana seedlings were grown for 9 months in enclosures in greenhouses at CO₂ concentrations of 350 or 750 $\mu\text{mol mol}^{-1}$ with either low (0.005 to 0.3 W M⁻²) or high (0.25 to 0.90 W M⁻²) ultraviolet-B (UV-B) irradiances. Total seedling dry weight decreased with high UV treatment but was unaffected by CO₂ enrichment. High UV treatment also shifted biomass partitioning in favor of leaf production. Both CO₂ and UV treatments decreased the dark respiration rate and light compensation point. High UV light inhibited photosynthesis at 350 but not at 750 $\mu\text{mol mol}^{-1}$ CO₂ due to a UV induced increase in ribulose-1,5-bisphosphate carboxylase/oxygenase efficiency and ribulose-1,5-bisphosphate regeneration. Stomatal density was increased by high UV irradiance but was unchanged by CO₂ enrichment.

KEYWORDS: ABSCISIC-ACID, C-3, CO₂, GAS-EXCHANGE, GROWTH, LEAVES, PLANTS, SEEDLINGS, STOMATAL CLOSURE, ULTRAVIOLET-B RADIATION

2270

Stewart, J., and C. Potvin. 1996. Effects of elevated CO₂ on an artificial grassland community: Competition, invasion and neighbourhood growth. *Functional Ecology* 10(2):157-166.

1. We analysed the effect of CO₂ enrichment on plant-plant interactions in an artificial community dominated by *Trifolium repens* and *Poa pratensis*. Plants were enriched either in open-tops or growth chambers. 2. Our main hypotheses were supported, i.e. elevated CO₂ increased the strength and number of plant-plant interactions and *Trifolium* benefited more than *Poa* from a high CO₂ concentration. However, responses

differed depending on whether plants were enriched in open-top or in growth chambers. These differences are discussed regarding possible density dependence. 3. This study emphasizes the importance of invasions in the dynamics of our artificial community. Invasiveness was best predicted by traits pertaining to space acquisition. 4. To provide insights into evolutionary processes, phenotypic plasticity and genetic correlation of individual traits were analysed across environments. Our results suggest that little opportunity had occurred for adaptive plasticity to evolve for most characters.

KEYWORDS: ABILITY, EVOLUTIONARY-THEORY, PLANTS

2271

Stiling, P., A.M. Rossi, B. Hungate, P. Dijkstra, C.R. Hinkle, W.M. Knott, and B. Drake. 1999. Decreased leaf-miner abundance in elevated CO₂: Reduced leaf quality and increased parasitoid attack. *Ecological Applications* 9(1):240-244.

Most studies on the effects of elevated CO₂ have focused on the effects on plant growth and ecosystem processes. Fewer studies have examined the effects of elevated CO₂ on herbivory, and of these, most have examined feeding rates in laboratory conditions. Our study takes advantage of an open-top CO₂ fertilization study in a Florida scrub-oak community to examine the effects of elevated CO₂ on herbivore densities, herbivore feeding rates, and levels of attack of herbivores by natural enemies. Higher atmospheric CO₂ concentration reduced plant foliar nitrogen concentrations, decreased abundance of leaf-mining insect herbivores, increased per capita leaf consumption by leafminers, and increased leaf miner mortality. As suggested by other authors, reduced foliar quality contributed to the increase in herbivore mortality, but only partly. The major factor increasing mortality was higher attack rate by parasitoids. Thus increasing CO₂ concentrations may reduce the survivorship of insect herbivores directly, by reducing plant quality, but also indirectly, by changing herbivore feeding and eliciting greater top-down pressure from natural enemies.

KEYWORDS: ATMOSPHERIC CO₂, CARBON DIOXIDE, DECIDUOUS TREES, DENSITY, INSECT HERBIVORE INTERACTIONS, LEPIDOPTERA, PERFORMANCE, PHYTOCHEMISTRY, PLANTS, POPULATION

2272

Stirling, C.M., P.A. Davey, T.G. Williams, and S.P. Long. 1997. Acclimation of photosynthesis to elevated CO₂ and temperature in five British native species of contrasting functional type. *Global Change Biology* 3(3):237-246.

Acclimation of photosynthesis to growth at elevated CO₂ concentration varies markedly between species. Species functionally classified as stress-tolerators (S) and ruderals (R), are thought to be incapable, or the least capable, of responding positively in terms of growth to elevated [CO₂]. Is this pattern of response also apparent in leaf photosynthesis of wild S- and R-strategists? Acclimatory loss of a photosynthetic and growth response to elevated [CO₂] is assumed to reflect limitation on capacity to utilize additional photosynthate. The doubling of pre-industrial global [CO₂] is expected to coincide with a 3 degrees C increase in mean temperature which could stimulate growth; will photosynthetic capacity at elevated [CO₂] be greater when the concurrent temperature increase is simulated? Five species from natural grassland of NW Europe and of contrasting ecological strategy were grown in hemispherical greenhouses, environmentally controlled to track the external microclimate. Within a replicated design, plants were grown at (i) current ambient [CO₂] and temperature, (ii) elevated [CO₂] (ambient + 340 $\mu\text{mol mol}^{-1}$) and ambient temperature, (iii) ambient [CO₂] and elevated temperature (ambient + 3 degrees C), or (iv) elevated [CO₂] and elevated temperature. After 75-104 days, the CO₂

response of light-saturated rates of photosynthesis ($A(\text{sat})$) was analysed in controlled-environment cuvettes in a field laboratory. There was no acclimatory loss of photosynthetic capacity with growth in elevated $[\text{CO}_2]$ or elevated temperature over this period in *Poa alpina* (S), *Bellis perennis* (R) or *Plantago lanceolata* (mixed C-S-R strategist), and a significant ($P < 0.05$) increase in capacity in *Helianthemum nummularium* (S) and *Poa annua* (R). Photosynthetic rates of leaves grown and measured in elevated $[\text{CO}_2]$ were therefore significantly higher than rates for leaves grown and measured in ambient $[\text{CO}_2]$, for all species. With the exception of *Poa alpina*, stomatal conductance and stomatal limitation on $A(\text{sat})$ showed no acclimatory response to growth in elevated $[\text{CO}_2]$. Carboxylation efficiency, determined from the initial slope of the response of $A(\text{sat})$ to intercellular CO_2 concentration was significantly increased by elevated $[\text{CO}_2]$ and elevated temperature in *H. nummularium*, implying a possible increase in *in vivo* RubisCO activity. Increased carboxylation efficiency of this species was also reflected by an increase in the CO_2 - and light- saturated rates of photosynthesis, indicating an increased capacity for regeneration of the primary CO_2 acceptor in photosynthesis. The results show that R-strategists and slow- growing S-strategists, are inherently capable of large increases in leaf photosynthetic capacity with growth in elevated $[\text{CO}_2]$ in contrast to expectations from growth studies. With the exception of *P. annua*, where there was a significant negative interaction between CO_2 and temperature, concurrent increase in growth temperature had little effect on this pattern of response.

KEYWORDS: ASSIMILATION, ATMOSPHERIC CO_2 , CARBON DIOXIDE, ENRICHMENT, EXPOSURE, GAS-EXCHANGE, GROWTH, PARTIAL-PRESSURE, PLANTS, RESPONSES

2273

Stirling, C.M., M. Heddell-Cowie, M.L. Jones, T.W. Ashenden, and T.H. Sparks. 1998. Effects of elevated CO_2 and temperature on growth and allometry of five native fast-growing annual species. *New Phytologist* 140(2):343-354.

Whereas much is known of the short-term growth response to elevated atmospheric CO_2 concentrations, $[\text{CO}_2](\text{elev})$, there is relatively little information on how the response of native species is modified by temperature, despite the fact that an increase in global mean temperature is expected to accompany the rise in $[\text{CO}_2]$. In this study, five functionally related annual native species were exposed to different combinations of ambient and elevated $[\text{CO}_2]$ and temperatures in order to assess their response in terms of growth and allometry. Fast-growing annuals were selected for the study because their growth responses could be assessed over a major portion of the plant's life cycle and in as short a period as 8 wk. Plants were grown in eight hemi-spherical glasshouses, programmed to track outside ambient conditions and provide a replicated experimental design. Treatments comprised (i) current ambient $[\text{CO}_2]$ and temperature, (ii) elevated $[\text{CO}_2]$ (ambient + 34 kPa), and ambient temperature (iii) ambient $[\text{CO}_2]$ and elevated temperature (ambient + 3 degrees C) and (iv) elevated $[\text{CO}_2]$ and elevated temperature (T degrees C-elev). All five species responded positively to $[\text{CO}_2](\text{elev})$, although the response was statistically significant for only one, *Poa annua* L. Averaged over all five species, $[\text{CO}_2](\text{elev})$ increased total plant biomass by 25 % ($P = 0.005$) at 56 d, reflecting a proportionally greater increase in leaf and stem mass relative to root weight. Elevated $[\text{CO}_2]$ had no effect on leaf area, either at the individual species level or overall. Elevated T degrees C, by contrast, had little effect on shoot growth but increased root mass on average by 43 % and leaf area by 22 %. Few interactions between elevated $[\text{CO}_2]$ and T degrees C were observed, with the CO_2 response generally greater at elevated than ambient T degrees C. Both $[\text{CO}_2](\text{elev})$ and T degrees C-elev resulted in a transient increase in relative growth rate, (RGR), during the first 14 d exposure and a 3 degrees C increase in temperature had no effect on the duration of the response. CO_2 stimulation of growth operated through a sustained increase in net assimilation rate. (NAR),

although the potential benefit to RGR was offset by a concurrent decline in leaf area ratio (LAR), as a result of a decrease in leaf area per unit leaf mass (SLA). The response to T degrees C-elev was generally opposite of that to $[\text{CO}_2](\text{elev})$. For example, T degrees C-elev increased LAR through an increase in SLA and this, rather than any effect on NAR, was the major factor responsible for the stimulation of RGR. Allometric analysis of CO_2 effects revealed that changes in allocation observed at individual harvests were due solely to changes associated with plant size. Elevated T degrees C, by contrast, had a direct effect on allocation patterns to leaves, with an increase in leaf area expansion relative to whole plant mass during the initial stages of growth and subsequent increased allocation of biomass away from leaves to other regions of the plant. No change in the allometric relation between roots and shoots were observed at either elevated $[\text{CO}_2]$ or T degrees C. We conclude, therefore, that allocation of biomass and morphological characteristics such as SLA, are relatively insensitive to $[\text{CO}_2]$, at least when analysed at the whole-plant level, and where changes have been observed, these are the product of comparing plants of the same age but different size.

KEYWORDS: ALLOCATION, CARBON DIOXIDE, ENRICHMENT, GRASSES, PHOTOSYNTHESIS, PLANTAGO-MAJOR, RESPIRATION, RESPONSES, SINK

2274

Stitt, M. 1991. Rising CO_2 levels and their potential significance for carbon flow in photosynthetic cells. *Plant, Cell and Environment* 14(8):741-762.

In the first part of this review, I discuss how we can predict the direct short-term effect of enhanced CO_2 on photosynthetic rate in C3 terrestrial plants. To do this, I consider: (1) to what extent enhanced CO_2 will stimulate or relieve demand on partial processes like carboxylation, light harvesting and electron transport, the Calvin cycle, and end-product synthesis; and (2) the extent to which these various processes actually control the rate of photosynthesis. I conclude that control is usually shared between Rubisco (which responds sensitively to CO_2) and other components (which respond less sensitively), and that photosynthesis will be stimulated by 25- 75% when the CO_2 concentration is doubled from 35 to 70 Pa. This is in good agreement with the published responses. In the next part of the review, I discuss the evidence that most plants undergo a gradual inhibition of photosynthesis during acclimation to enhanced CO_2 . I argue that this is related to an inadequate demand for carbohydrate in the remainder of the plant. Differences in the long-term response to CO_2 may be explained by differences in the sink-source status of plants. depending upon the species, the developmental stage, and the developmental conditions. In the third part of the review, I consider the biochemical mechanisms which are involved in 'sink' regulation of photosynthesis. Accumulating carbohydrate could lead to a direct inhibition of photosynthesis, involving mechanical damage by large starch grains or Pi-limitation due to inhibition of sucrose synthesis. I argue that Pi is important in the short-term regulation of partitioning to sucrose and starch, but that its contribution to 'sink' regulation has not yet been conclusively demonstrated. Indirect or 'adaptive' regulation of photosynthesis is probably more important, involving decreases in amounts of key photosynthetic enzymes, including Rubisco. This decreases the rate of photosynthesis, and potentially would allow resources (e.g. amino acids) to be remobilized from the leaves and reinvested in sink growth to readjust the sink-source balance. In the final part of the review, I argue that similar changes of Rubisco and, possibly, other proteins are probably also involved during acclimation to high CO_2 .

KEYWORDS: CALVIN CYCLE ENZYMES, DRY-MATTER PRODUCTION, FLUX-CONTROL COEFFICIENTS, HIGH ATMOSPHERIC CO_2 , LONG-TERM EXPOSURE, PHASEOLUS-VULGARIS L, RIBULOSE BISPHOSPHATE CARBOXYLASE,

2275

Stütt, M., and A. Krapp. 1999. The interaction between elevated carbon dioxide and nitrogen nutrition: the physiological and molecular background. *Plant, Cell and Environment* 22(6):583-621.

This review first summarizes the numerous studies that have described the interaction between the nitrogen supply and the response of photosynthesis, metabolism and growth to elevated [CO₂]. The initial stimulation of photosynthesis in elevated [CO₂] is often followed by a decline of photosynthesis, that is typically accompanied by a decrease of ribulose-1,5- bisphosphate carboxylase/oxygenase (Rubisco), an accumulation of carbohydrate especially starch, and a decrease of the nitrogen concentration in the plant. These changes are particularly marked when the nitrogen supply is low, whereas when the nitrogen supply is adequate there is no acclimation of photosynthesis, no major decrease in the internal concentration of nitrogen or the levels of nitrogen metabolites, and growth is stimulated markedly. Second, emerging evidence is discussed that signals derived from nitrate and nitrogen metabolites such as glutamine act to regulate the expression of genes involved in nitrate and ammonium uptake and assimilation? organic acid synthesis and starch accumulation, to modulate the sugar-mediated repression of the expression of genes involved in photosynthesis, and to modulate whole plant events including shoot-root allocation, root architecture and flowering. Third, increased rates of growth in elevated [CO₂] will require higher rates of inorganic nitrogen uptake and assimilation. Recent evidence is discussed that an increased supply of sugars can increase the rates of nitrate and ammonium uptake and assimilation, the synthesis of organic acid accepters, and the synthesis of amino acids. Fourth, interpretation of experiments in elevated [CO₂] requires that the nitrogen status of the plants is monitored. The suitability of different criteria to assess the plant nitrogen status is critically discussed. Finally the review returns to experiments with elevated [CO₂] and discusses the following topics: is, and if so how, are nitrate and ammonium uptake and metabolism stimulated in elevated [CO₂], and does the result depend on the nitrogen supply? Is acclimation of photosynthesis the result of sugar- mediated repression of gene expression, end-product feedback of photosynthesis, nitrogen-induced senescence, or ontogenetic drift? Is the accumulation of starch a passive response to increased carbohydrate formation, or is it triggered by changes in the nutrient status? How do changes in sugar production and inorganic nitrogen assimilation interact in different conditions and at different stages of the life history to determine the response of whole plant growth and allocation to elevated [CO₂]?

KEYWORDS: ADP-GLUCOSE PYROPHOSPHORYLASE, ARABIDOPSIS-THALIANA L, ATMOSPHERIC CO₂ ENRICHMENT, CALVIN CYCLE ENZYMES, DEPENDENT GLUTAMATE SYNTHASE, NITRATE REDUCTASE-ACTIVITY, PHASEOLUS-VULGARIS L, RIBULOSE-1;5-BISPHOSPHATE CARBOXYLASE-OXYGENASE, SUCROSE PHOSPHATE SYNTHASE, TRANSGENIC TOBACCO PLANTS

2276

Stütt, M., W.P. Quick, U. Schurr, E.D. Schulze, S.R. Rodermel, and L. Bogorad. 1991. Decreased ribulose-1,5-bisphosphate carboxylase-oxygenase in transgenic tobacco transformed with antisense rbcS .2. Flux- control coefficients for photosynthesis in varying light, CO₂, and air humidity. *Planta* 183(4):555-566.

Transgenic tobacco (*Nicotiana tabacum* L.) plants transformed with 'antisense' rbcS to produce a series of plants with a progressive decrease in the amount of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) have been used to investigate the contribution of Rubisco to

the control of photosynthesis at different irradiance, CO₂ concentrations and vapour-pressure deficits. Assimilation rates, transpiration, the internal CO₂ concentration and chlorophyll fluorescence were measured in each plant. (i) The flux-control coefficient of Rubisco was estimated from the slope of the plot of Rubisco content versus assimilation rate. The flux-control coefficient had a value of 0.8 or more in high irradiance, (1050 μmol m⁻² s⁻¹), low-vapour pressure deficit (4 mbar) and ambient CO₂ (350-μ-bar). Control was marginal in enhanced CO₂ (450-μ-bar) or low light (310 μmol m⁻² s⁻¹) and was also decreased at high vapour- pressure deficit (17 mbar). No control was exerted in 5% CO₂. (ii) The flux-control coefficients of Rubisco were compared with the fractional demand placed on the calculated available Rubisco capacity. Only a marginal control on photosynthetic flux is exerted by Rubisco until over 50% of the available capacity is being used. Control increases as utilisation rises to 80%, and approaches unity (i.e. strict limitation) when more than 80% of the available capacity is being used. (iii) In low light, plants with reduced Rubisco have very high energy-dependent quenching of chlorophyll fluorescence (qE) and a decreased apparent quantum yield. It is argued that Rubisco still exerts marginal control in these conditions because decreased Rubisco leads to increased thylakoid energisation and high-energy dependent dissipation of light energy, and lower light-harvesting efficiency. (iv) The flux-control coefficient of stomata for photosynthesis was calculated from the flux-control coefficient of Rubisco and the internal CO₂ concentration, by applying the connectivity theorem. Control by the stomata varies between zero and about 0.25. It is increased by increased irradiance, decreased CO₂ or decreased vapour-pressure deficit. (v) Photosynthetic oscillations in saturating irradiance and CO₂ are suppressed in decreased- activity transformants before the steady-state rate of photosynthesis is affected. This provides direct evidence that these oscillations reveal the presence of "excess" Rubisco. (vi) Comparison of the flux-control coefficients of Rubisco with mechanistic models of photosynthesis provides direct support for the reliability of these models in conditions where Rubisco has a flux-control coefficient approach unity (i.e. "limits" photosynthesis), but also indicates that these models are less useful in conditions where control is shared between Rubisco and other components of the photosynthetic apparatus.

KEYWORDS: C-3 PLANTS, FIXATION, LEAVES, LIMITATIONS, METABOLISM, NITROGEN, PHOSPHATE

2277

Stocker, R., C. Korner, B. Schmid, P.A. Niklaus, and P.W. Leadley. 1999. A field study of the effects of elevated CO₂ and plant species diversity on ecosystem-level gas exchange in a planted calcareous grassland. *Global Change Biology* 5(1):95-105.

The relationship between plant species diversity and ecosystem CO₂ and water vapour fluxes was investigated for planted calcareous grassland communities composed of 5, 12, or 32 species assembled from the native plant species pool. These diversity manipulations were done in factorial combination with a CO₂ enrichment experiment in order to investigate the degree to which ecosystem responses to elevated CO₂ are altered by a loss of plant diversity. Ecosystem CO₂ and H₂O fluxes were measured over several 24-h periods during the 1994 and 1995 growing seasons. Ecosystem CO₂ assimilation on a ground area basis decreased with decreasing plant diversity in the first year and this was related to a decline in above-ground plant biomass. In the second year, however, CO₂ assimilation was not affected by diversity, and this corresponded to the disappearance of a diversity effect on above-ground biomass. Irrespective of diversity treatment, CO₂ assimilation on a ground area basis was linearly related to peak aboveground biomass in both years. Elevated CO₂ significantly increased ecosystem CO₂ assimilation in both years with no interaction between diversity and CO₂ treatment, and no corresponding increase in above-ground biomass. There were no significant effects of diversity on water vapour nux, which was measured only in the second year. There were indications of a small CO₂ effect on

water vapour flux (3-9% lower at elevated CO₂ depending on the light level). Our findings suggest that decreasing plant species diversity may substantially decrease ecosystem CO₂ assimilation during the establishment of such planted calcareous grassland communities, but also suggest that this effect may not persist. In addition, we find no evidence that plant species diversity alters the response of ecosystem CO₂ assimilation to elevated CO₂.

KEYWORDS: ALTER, BIODIVERSITY, CARBON, ECOLOGY, PERFORMANCE, PRODUCTIVITY, STOMATAL RESPONSES, TRANSPIRATION

2278

Stocker, R., P.W. Leadley, and C. Korner. 1997. Carbon and water fluxes in a calcareous grassland under elevated CO₂. *Functional Ecology* 11(2):222-230.

1. As part of a long-term study of the effects of elevated CO₂ on biodiversity and ecosystem function in a calcareous grassland, we measured ecosystem carbon dioxide and water- vapour fluxes over 24-h periods during the 1994 and 1995 growing seasons. Data were used to derive CO₂ and H₂O gas- exchange response functions to quantum flux density (QFD). 2. The relative increase in net ecosystem CO₂ flux (NEC) owing to CO₂ enrichment increased as QFD rose. Daytime NEC at high QFD under elevated CO₂ increased by 25% to 60%, with the greatest increases in the spring and after mowing in June when above-ground biomass was lowest. There was much less stimulation of NEC in early June and again in October when the canopy was fully developed. Night-time NEC was not significantly altered under elevated CO₂. 3. Short-term reversal of CO₂ concentrations between treatments after two seasons of CO₂ exposure provided evidence for a 50% downward adjustment of NEC expressed per unit above-ground plant dry weight. However, when expressed on a land area basis, this difference disappeared because of a c. 20% increase in above-ground biomass under elevated CO₂. 4. Ecosystem evapotranspiration (ET) was not significantly altered by elevated CO₂ when averaged over all measurement dates and positions. However, ET was reduced 3-18% at high QFD in plots at the top of the slope at our study site. In summary, CO₂ enrichment resulted in a large stimulation of ecosystem CO₂ capture, especially during periods of a large demand of carbon in relationship to its supply, and resulted in a relatively small and variable effect on ecosystem water consumption.

KEYWORDS: ATMOSPHERIC CO₂, CARBOXYLASE ACTIVITY, DIOXIDE, GAS-EXCHANGE, GROWTH, PARTIAL-PRESSURE, PHOTOSYNTHESIS, PLANT, RISING CO₂, TUSsock TUNDRA

2279

Stocklin, J., and C. Korner. 1999. Interactive effects of elevated CO₂, P availability and legume presence on calcareous grassland: results of a glasshouse experiment. *Functional Ecology* 13(2):200-209.

1. We investigated the interactive effects of elevated CO₂, supply of phosphorus (P) and legume presence in model communities of calcareous grassland. Half of the communities contained six graminoids and eight non-legume forb species. In the other half, four non-legume forbs were replaced by legumes. 2. Ecosystem responses. Above-ground phytomass (>5 cm) hardly responded to elevated CO₂ alone. However, when P and legumes were combined, the CO₂ effect on above-ground community phytomass in year two was a stimulation of 45% ($P < 0.001$). Below-ground community dry matter was stimulated by elevated CO₂ alone by + 36% ($P < 0.01$), but was only + 20% ($P < 0.05$) when legumes were present and P was added. At the final (late season) harvest the mean effect of elevated CO₂ on total above- and below-ground phytomass was + 23% ($P < 0.001$) and revealed no significant interactions among treatment combinations, because above- and

belowground effects of CO₂ enrichment had opposite directions. 3. Functional group responses. When legumes were absent, graminoids increased their total above- and below-ground phytomass in elevated CO₂ by 60% ($P < 0.001$) but there was no increase when legumes were present. The response of forbs to CO₂ was not significant, irrespective of co-treatment. Legumes, however, were significantly stimulated by P supply and their CO₂ response was much larger when P was added (+ 55%, $P < 0.01$ vs + 25%, NS). 4. Species responses. CO₂ effects on species ranged from highly positive (+ 143%) to moderately negative (- 43%). 5. Our results demonstrate that the effect of CO₂ enrichment in such natural grassland communities will be low on above-ground phytomass and largely below-ground if no additional nutrients are provided. N-2- fixing legumes appear to be crucial for the community response to elevated CO₂ but legume responsiveness is largely controlled by P availability.

KEYWORDS: CARBON BALANCE, CHALK GRASSLAND, GROWTH-RESPONSE, LEVEL RESPONSES, LOLIUM-PERENNE L, NITROGEN-FIXATION, OLD-FIELD MICROCOSMS, PLANTS, STOMATAL RESPONSES, TRIFOLIUM-REPENS L

2280

Stocklin, J., P.W. Leadley, and C. Korner. 1997. Community and species level responses to elevated CO₂ in designed calcareous grassland communities. *Acta Oecologica-International Journal of Ecology* 18(3):241-248.

We present a synthesis of two independent glasshouse experiments in which we investigated the short term response of model communities of calcareous grassland species to CO₂- enrichment. Communities consisted of six species in the first study and of 14 species in the second study. Communities were grown in containers filled with ca. 20 liters of natural soil. Total aboveground biomass production was increased by 14% (n.s., $p=0.21$) in the first study and by 8.5% ($p=0.03$) in the second study. This community level response was due to a significant stimulation of growth in 2 and 5 species, respectively. In each of the experiments, one species responded negatively to CO₂-enrichment. The remaining species, including all legumes, remained unaffected by CO₂-enrichment. Positive or negative responding species did not belong to specific functional groups, hence responses could not have been predicted from a priori knowledge of individual plant traits. *Bromus erectus*, which is the dominant species in calcareous grasslands of the Jura mountains, did not exhibit a CO₂- response at the species level, but genotype-specific responses in this species varied significantly and included positive as well as negative responses. No such genotypic differentiation of CO₂-response was observed in *Festuca ovina*. In the long term, we expect directional selection of positively responding genotypes and shifts in species composition to alter both population and community structure of calcareous grasslands - a conclusion that may also hold for other diverse plant communities.

KEYWORDS: ABANDONMENT, GROWTH, UNFERTILIZED MOWN MEADOWS

2281

Stocklin, J., K. Schweizer, and C. Korner. 1998. Effects of elevated CO₂ and phosphorus addition on productivity and community composition of intact monoliths from calcareous grassland. *Oecologia* 116(1-2):50-56.

We investigated the effects of elevated CO₂ (600 $\mu\text{mol l}^{-1}$ vs 350 $\mu\text{mol l}^{-1}$) and phosphorus supply (1 g P m⁻² year⁻¹ vs unfertilized) on intact monoliths from species-rich calcareous grassland in a greenhouse. Aboveground community dry mass remained almost unaffected by elevated CO₂ in the first year (+ 6%, n.s.), but was significantly stimulated by CO₂ enrichment in year two (+26%, $P < 0.01$). Among

functional groups, only graminoids contributed significantly to this increase. The effect of phosphorus alone on community biomass was small in both years and marginally significant only when analyzed with MANOVA (+6% in year one, +9% in year two, 0.1 greater than or equal to $P > 0.05$). Belowground biomass and stubble after two seasons were not different in elevated CO₂ and when P was added. The small initial increase in aboveground community biomass under elevated CO₂ is explained by the fact that some species, in particular *Carex flacca*, responded very positively right from the beginning, while others, especially the dominant *Bromus erectus*, responded negatively to CO₂ enrichment. Shifts in community composition towards more responsive species explain the much larger CO₂ response in the second year. These shifts, i.e., a decline in xerophytic elements (*B. erectus*) and an increase in mesophytic grasses and legumes occurred independently of treatments in all monoliths but were accelerated significantly by elevated CO₂. The difference in average biomass production at elevated compared to ambient CO₂ was higher when P was supplied (at the community level the CO₂ response was enhanced from 20% to 33% when P was added, in graminoids from 17% to 27%, in legumes from 4% to 60% and in *C. flacca* from 120% to 298% by year two). Based on observations in this and similar studies, we suggest that interactions between CO₂ concentration, species presence, and nutrient availability will govern community responses to elevated CO₂.

KEYWORDS: BIOMASS, CHALK GRASSLAND, ECOSYSTEMS, ENRICHMENT, GROWTH, LEVEL RESPONSES, PLANTS

2282

Stoffella, P.J., Y.C. Li, R.R. Pelosi, and A.M. Hamner. 1995. Citrus rootstock and carbon-dioxide enriched irrigation influence on seedling emergence, growth, and nutrient content. *Journal of Plant Nutrition* 18(7):1439-1448.

Seeds of Carrizo citrange (*Citrus senensis* (L.) Osb. X *Poncirus trifolliata* (L.), Cleopatra mandarin (*C. reticulata* Bianco), Sour orange (*C. aurantium* L.), and Rough lemon (*C. limon* (Burm f.) were sown in trays, irrigated without or with enriched Carbon dioxide (CO₂) (1,362 mg L⁻¹) and evaluated for seedling emergence, growth, and nutrient contents. Rough lemon had a faster rate and higher percent emergence than the other rootstocks. Carrizo citrange had thicker stem diameters and taller seedlings than other rootstocks. Cleopatra mandarin had the smallest seedling shoot and root weights and larger shoot:root ratios than Rough lemon and Sour orange. Carrizo citrange and Cleopatra mandarin had higher leaf chlorophyll-a and total chlorophyll content than Rough lemon or Sour orange. Carbon dioxide enriched irrigation had no effects on emergence or seedling growth variables except lower root weight. Lower media pH (6.90 versus 5.65), attributed to CO₂ enriched irrigation, may have adversely affected root growth as compared to shoot characteristics. Leaf nutrient contents generally differed between rootstocks but were not affected by CO₂ enriched water except for higher Zn and lower Mn contents. These results indicate that citrus seedling emergence, subsequent growth and leaf nutrient content differed between rootstocks but there are no beneficial effect from CO₂ enriched irrigation.

KEYWORDS: CO₂, FIELD, ROOT ZONE, TOMATO, WATER

2283

Storlie, C.A., and J.R. Heckman. 1996. Bell pepper yield response to carbonated irrigation water. *Journal of Plant Nutrition* 19(10-11):1477-1484.

Field studies were conducted to determine the influence of carbonated irrigation water on bell pepper (*Capsicum annuum* L.) yield, plant nutrient status, canopy carbon dioxide (CO₂) concentration, and soil pH. Marketable yield, early yield, marketable fruit size distribution, and

plant nutrient status were unaffected by carbonated irrigation water. Air CO₂ concentration in the lowest portion of the canopy increased during irrigation events, but returned to the ambient CO₂ concentration shortly after irrigation ceased. The effect of carbonated irrigation water on soil pH was marginal and unpredictable.

KEYWORDS: CO₂, DIOXIDE ENRICHMENT, FIELD, FIXATION, GROWTH, POTATO PLANTS, ROOT ZONE, TOMATO

2284

Strain, B.R., and R.B. Thomas. 1992. Field-measurements of CO₂ enhancement and climate change in natural vegetation. *Water, Air, and Soil Pollution* 64(1-2):45-60.

It is generally assumed that healthy, natural ecosystems have the potential to sequester carbon under favorable environmental conditions. There is also evidence that CO₂ acts as a plant fertilizer. It is of interest to know if these assumptions are valid and how natural systems might respond under future scenarios of CO₂ increase and possible climate changes. Few measurements of the effects of CO₂ and global climate change have been made on "natural" ecosystems under realistic field conditions. Most measurements have been conducted in the synthetic environments of totally controlled greenhouses and growth chambers. Several lines of evidence indicate that controlled environment studies using plants growing in pots induce experimental artifacts that reduce confidence in the use of results for prediction of future global responses. Open top chambers are being used in several autecological field studies in an attempt to obtain more realistic field environments. A few field microcosm studies have been completed and a system for the free air release of CO₂ has been applied in cotton fields. Unfortunately, the requirement of large amounts of CO₂ and financial restrictions have precluded the initiation of larger scale field studies in natural vegetation. This paper lists and summarizes the best field studies available but draws heavily on studies from artificial environments and conditions in an attempt to summarize knowledge of global environmental change on forests and other non-agricultural ecosystems. Finally the paper concludes that there is a need for the development and application of equipment for field measurements in several representative natural ecosystems and makes specific recommendation of the creation of a tropical research center.

KEYWORDS: ALASKAN TUNDRA, ATMOSPHERIC CARBON-DIOXIDE, DIFFERENT IRRADIANCE LEVELS, ELEVATED CO₂, ESTUARINE MARSH, LIQUIDAMBAR- STYRACIFLUA, MINERAL NUTRITION, PINUS-TAEDA SEEDLINGS, TUSsock TUNDRA, WATER-STRESS

2285

Strand, M., D.A. Herms, M.P. Ayres, M.E. Kabiske, M.G. Kaufman, E.D. Walker, K.S. Pregitzer, and R.W. Merritt. 1999. Effects of atmospheric CO₂, light availability and tree species on the quality of leaf detritus as a resource for treehole mosquitoes. *Oikos* 84(2):277-283.

Elevated CO₂ could alter the productivity of heterotrophic aquatic ecosystems through effects on allochthonous litter inputs. The effects of atmospheric CO₂ concentration, light availability to trees and tree species, on leaf detritus quality as a food resource for eastern treehole mosquitoes (*Aedes triseriatus*) were examined. Larvae were reared in laboratory microcosms (simulated treeholes) with naturally- senesced, abscised foliage from seedlings of red oak (*Quercus rubra*) and paper birch (*Betula papyrifera*) grown in ambient and elevated atmospheric CO₂ environments. Elevated CO₂ did not have significant effects on any measure of mosquito performance. In contrast, host species and light availability had dramatic effects on mosquito development time and survival; light availability had additional effects on adult size. Mosquito reproductive potential (+/- SE) averaged 8.4 +/- 1.5 females female(-1)

generation(-1) when litter input was from birch-sun leaves, but was 19.6 +/- 1.8 when the litter was from birch-shade leaves and 13.0 +/- 1.8 when from oak-sun leaves. Mosquito development time was nearly halved when the litter input was from oak-sun leaves versus birch-sun leaves, suggesting a potential for even greater demographic effects (e.g. two generations per year instead of one could yield a 20- fold increase in annual growth rate). Trophic transfer rates (mg insect detritivore g litter(-1) d(-1)) were 3-fold greater on birch-shade leaves than on birch-sun leaves. Changes in insolation and tree species composition can have important consequences for forest ecosystems, because of effects on litter quality that impact microbial saprobes and, ultimately, invertebrate detritivores.

KEYWORDS: *AEDES-TRISERIATUS DIPTERA, BETULA-PENDULA ROTH, CARBON NUTRIENT BALANCE, CONDENSED TANNINS, DECOMPOSITION RATES, ELEVATED CO2, HOLE ECOSYSTEMS, LITTER QUALITY, SECONDARY METABOLITES, TERRESTRIAL ECOSYSTEMS*

2286

Street-Perrott, F.A., Y.S. Huang, R.A. Perrott, G. Eglinton, P. Barker, L. BenKhelifa, D.D. Harkness, and D.O. Olago. 1997. Impact of lower atmospheric carbon dioxide on tropical mountain ecosystems. *Science* 278(5342):1422-1426.

Carbon-isotope values of bulk organic matter from high-altitude lakes on Mount Kenya and Mount Elgon, East Africa, were 10 to 14 per mil higher during glacial times than they are today. Compound-specific isotope analyses of leaf waxes and algal biomarkers show that organisms possessing CO₂-concentrating mechanisms, including C-4 grasses and freshwater algae, were primarily responsible for this large increase. Carbon limitation due to lower ambient CO₂ partial pressures had a significant impact on the distribution of forest on the tropical mountains, in addition to climate. Hence, tree line elevation should not be used to infer palaeotemperatures.

KEYWORDS: *CO2, HYDROCARBONS, ICE CORE, ISOTOPE FRACTIONATION, ORGANIC-MATTER, PHYTOPLANKTON, PLANTS, QUATERNARY, SACRED-LAKE, SEDIMENTS*

2287

Stronach, I.M., S.C. Clifford, A.D. Mohamed, P.R. Singletonjones, S.N. Azamali, and N.M.J. Crout. 1994. The effects of elevated carbon-dioxide, temperature and soil- moisture on the water-use of stands of groundnut (*arachis- hypogaea* L). *Journal of Experimental Botany* 45(280):1633-1638.

Stands of groundnut (*Arachis hypogaea* L. cv. Kadiri 3) were grown in controlled environment glasshouses at two mean air temperatures (28 degrees C and 32 degrees C), two atmospheric CO₂ concentrations (375 ppmv and 700 ppmv) and two soil moisture treatments (irrigated weekly to field capacity or allowed to dry from 22 d after sowing). The transpiration equivalent, Omega(W) (g kPa kg(-1))-the product of the accumulated biomass/transpired water ratio and the saturation deficit-was calculated for all the treatments using aboveground harvest, root core and neutron probe measurements. Neither temperature nor soil moisture treatment was found to have an effect on Omega(W). Increased CO₂ concentration raised Omega(W) from 6.21 +/- 0.30 to 7.67 +/- 0.29 g kPa kg(-1), an increase of 24% (P < 0.005). The importance of accounting for root material and pod composition when calculating Omega(W) was highlighted.

KEYWORDS: *CO2, CROPS, USE EFFICIENCY*

2288

Stryiewski, E.C., and D.A. Vieglais. 1995. Changes in leaf structure of 3 native florida plant-species grown in elevated co2 concentrations. *Plant Physiology* 108(2):63.

2289

Stuhlfauth, T., and H.P. Fock. 1990. Effect of whole season CO₂ enrichment on the cultivation of a medicinal plant, *digitalis-lanata*. *Journal of Agronomy and Crop Science-Zeitschrift Fur Acker Und Pflanzenbau* 164(3):168-173.

2290

Stulen, I., and J. Denhertog. 1993. Root-growth and functioning under atmospheric co2 enrichment. *Vegetatio* 104:99-115.

This paper examines the extent to which atmospheric CO₂ enrichment may influence growth of plant roots and function in terms of uptake of water and nutrients, and carbon allocation towards symbionts. It is concluded that changes in dry matter allocation greatly depend on the experimental conditions during the experiment, the growth phase of the plant, and its morphological characteristics. Under non-limiting conditions of water and nutrients for growth, dry matter partitioning to the root is not changed by CO₂ enrichment. The increase in root/shoot ratio, frequently observed under limiting conditions of water and/or nutrients, enables the plant to explore a greater soil volume, and hence acquire more water and nutrients. However, more data on changes in dry matter allocation within the root due to atmospheric CO₂ are needed. It is concluded that nitrogen fixation is favored by CO₂ enrichment since nodule mass is increased, concomitant with an increase in root length. The papers available so far on the influence of CO₂ enrichment on mycorrhizal functioning suggest that carbon allocation to the roots might be increased, but also here more experiments are needed.

KEYWORDS: *CARBOHYDRATE CONTENT, CARBON-DIOXIDE ENRICHMENT, LIQUIDAMBAR- STYRACIFLUA, MINERAL NUTRITION, NUTRIENT CONCENTRATION, PINUS-TAEDA SEEDLINGS, PISUM-SATIVUM, PLANT GROWTH, SOYBEAN PLANTS, WATER-STRESS*

2291

Stutte, G.W., N.C. Yorio, and R.M. Wheeler. 1996. Interacting effects of photoperiod and photosynthetic photon flux on net carbon assimilation and starch accumulation in potato leaves. *Journal of the American Society for Horticultural Science* 121(2):264-268.

The effect of photoperiod (PP) on net carbon assimilation rate (A(net)) and starch accumulation in newly mature canopy leaves of 'Norland' potato (*Solanum tuberosum* L.) was determined under high (412 proportional to mol .(m-)2 . s(-1)) and low (263 proportional to mol . m(-2). s(-1)) photosynthetic photon flux (PPF) conditions. The A(net) decreased from 13.9 to 11.6 and 9.3 mu mol . m(-2). s(-1), and leaf starch increased from 70 to 129 and 118 mg . g(-1) drymass (DM) as photoperiod (PP) was increased from 12/12 to 18/6, and 24/0, respectively. Longer PP had a greater effect with high PPF conditions than with low PPF treatments, with high PPF showing greater decline in A(net). Photoperiod did not affect either the CO₂ compensation point (50 mu mol . mol(-1)) or CO₂ saturation point (1100-1200 mu mol . mol(-1)) for A(net). These results show an apparent limit to the amount of starch that can be stored (approximate to 15% DM) in potato leaves. An apparent feedback mechanism exists for regulating A(net) under high PPF, high CO₂ and long PP, but there was no correlation between A(net) and starch concentration in individual leaves. This suggests that maximum A(net) cannot be sustained with elevated CO₂ conditions under long PP (greater than or equal to 12 hours) and high PPF

conditions. If a physiological limit exists for the fixation and transport of carbon, then increasing photoperiod and light intensity under high CO₂ conditions is not the most appropriate means to maximize the yield of potatoes.

KEYWORDS: GROWTH, LIFE SUPPORT SYSTEMS, LIGHT, PLANTS, SOLANUM TUBEROSUM L, SPACE

2292

Sukumar, R., H.S. Suresh, and R. Ramesh. 1995. Climate change and its impact on tropical montane ecosystems in southern India. *Journal of Biogeography* 22(2-3):533-536.

The montane regions (>2000 m MSL) of the Western Ghats in southern India feature stunted evergreen forests (C3 plant type) interspersed with extensive grasslands (C3 or C4 plant types). We have studied the vegetational history of this ecosystem in relation to climate change during the late Quaternary through stable-carbon isotope analysis of peat deposits as indicators of C3 or C4 plant types. Grasslands (of C4 type) were predominant during the last glacial maximum (20- 18 kyr sp) and again during 6-3.5 kyr sp, while forest and possibly C3 grassland expanded during the deglaciation, attaining their peak distribution at 10 kyr sp. The shift in C3 and C4 plant types seems related to changes in moisture and atmospheric CO₂, with lower moisture and CO₂ levels favouring the latter plant types. The oscillating climate and vegetation has influenced the structure and composition of the montane ecosystem. Plant diversity of the near-pristine montane forests is relatively lower than other comparable sites in the neotropics. The implications of global change on the tropical montane ecosystem, in particular the composition of the angiosperm and vertebrate communities, are discussed. In particular, an expansion of montane forest and replacement of C4 with C3 grassland can be expected. Human impact on the natural vegetation, such as conversion of grasslands to monoculture plantations of wattle and eucalypts may, however, interfere with natural succession caused by global climate change. Endemic mammals such as the Nilgiri tahr would face increased risk of extinction.

KEYWORDS: ICE-AGE, ISOTOPE EVIDENCE, KENYA, POLLEN, RECORD

2293

Sullivan, J.H. 1997. Effects of increasing UV-B radiation and atmospheric CO₂ on photosynthesis and growth: Implications for terrestrial ecosystems. *Plant Ecology* 128(1-2):194-206.

Increases in UV-B radiation reaching the earth as a result of stratospheric ozone depletion will most likely accompany increases in atmospheric CO₂ concentrations. Many studies have examined the effects of each factor independently, but few have evaluated the combined effects of both UV-B radiation and elevated CO₂. In general the results of such studies have shown independent effects on growth or seed yield. Although interspecific variation is large, high levels of UV-B radiation tends to reduce plant growth in sensitive species, while CO₂ enrichment tends to promote growth in most C-3 species. However, most previous studies have not looked at temporal effects or at the relationship between photosynthetic acclimation to CO₂ and possible photosynthetic limitations imposed by UV-B radiation. Elevated CO₂ may provide some protection against UV-B for some species. In contrast, UV-B radiation may limit the ability to exploit elevated CO₂ in other species. Interactions between the effects of CO₂ enrichment and UV-B radiation exposure have also been shown for biomass allocation. Effects on both biomass allocation and photosynthetic acclimation may be important to ecosystem structure in terms of seedling establishment, competition and reproductive output. Few studies have evaluated ecosystem processes such as decomposition or nutrient cycling. Interactive effects may be subtle and species specific but should not be ignored in the assessment

of the potential impacts of increases in CO₂ and W-B radiation on plants.

KEYWORDS: BARLEY PRIMARY LEAVES, ELEVATED CARBON-DIOXIDE, HERBIVORE INTERACTIONS, LEAF EXPANSION, LIQUIDAMBAR- STYRACIFLUA, OZONE DEPLETION, PHOTON FLUX- DENSITY, PINUS-TAEDA SEEDLINGS, PLANT COMPETITION, SCIRPUS- OLNEYI

2294

Sullivan, J.H., and A.H. Teramura. 1994. The effects of uv-b radiation on loblolly-pine .3. Interaction with co2 enhancement. *Plant, Cell and Environment* 17(3):311-317.

Projected depletions in the stratospheric ozone layer will result in increases in solar ultraviolet-B radiation (290- 320nm) reaching the earth's surface. These increases will likely occur in concert with other environmental changes such as increases in atmospheric carbon dioxide concentrations. Currently very little information is available on the effectiveness of UV-B radiation within a CO₂-enriched atmosphere, and this is especially true for trees. Loblolly pine (*Pinus taeda* L.) seedlings were grown in a factorial experiment at the Duke University Phytotron with either 0, 8.8 or 13.8 kJ m⁻² of biologically effective UV-B radiation (UV- B-BE) The CO₂ concentrations used were 350 and 650 μ mol mol⁻¹. Measurements of chlorophyll fluorescence were made at 5- week intervals and photosynthetic oxygen evolution and leaf pigments were measured after 22 weeks, prior to harvest. The results of this study demonstrated a clear growth response to CO₂ enrichment but neither photosynthetic capacity nor quantum efficiency were altered by CO₂. The higher UV-B irradiance reduced total biomass by about 12% at both CO₂ levels but biomass partitioning was altered by the interaction of CO₂ and UV-B radiation. Dry matter was preferentially allocated to shoot components by UV-B radiation at 350 μ mol mol⁻¹ CO₂ and towards root components at 650 μ mol mol⁻¹ CO₂. These subtle effects on biomass allocation could be important in the future to seedling establishment and competitive interactions in natural as well as agricultural communities.

KEYWORDS: COMPETITION, ENRICHMENT, GROWN SEEDLINGS, HIGHER-PLANTS, IRRADIANCE, LIQUIDAMBAR- STYRACIFLUA, PHOTOSYNTHESIS, TAEDA SEEDLINGS, ULTRAVIOLET-B, VISIBLE-LIGHT

2295

Sultemeyer, D. 1997. Changes in the CO₂ concentrating mechanism during the cell cycle in *Dunaliella tertiolecta*. *Botanica Acta* 110(1):55-61.

Synchronised cells of *Dunaliella tertiolecta* were used to investigate the expression of the CO₂ concentrating mechanism over the cell cycle during growth in either ambient air (low Ci cells) or air enriched with 5% CO₂ (high Ci cells). The cultures were analysed for extracellular carbonic anhydrase activity, affinity of photosynthesis for inorganic carbon (Ci) and the ability to accumulate Ci. In high Ci cells, carbonic anhydrase activity changed between 2-4 units mg⁻¹ Chl during the light-dark rhythm showing no clear periodicity. Similarly, the apparent affinity for Ci remained rather constant over the cell cycle. This was judged from the Ci concentrations required for half maximum rate of photosynthesis (K-1/2(Ci)) of 72-80 μ M. In the same cells the accumulation ratio of internal Ci versus external Ci ranged between 5 and 9.5 without a clear rhythm. In contrast, these parameters showed distinct periodical changes in synchronised low Ci cells. Carbonic anhydrase activity changed from 10 to 350 units mg⁻¹ Chl with maximum and minimum activities occurring in the middle and at the end of the light period, respectively. The K-1/2(Ci) values showed similar periodicity ranging between 13-36 μ M. In addition the

accumulation ratio increased up to 30 in the middle of illumination and decreased to its lowest level of 12 at the end of the light period. These results indicate the presence of a common step in regulating the induction of the measured parameters and that light is not an absolute requirement for the induction of the CO₂ concentrating mechanism in synchronous low CO₂ grown cells of *Dunaliella tertiolecta*.

KEYWORDS: ADAPTATION, BICARBONATE, CARBONIC-ANHYDRASE ACTIVITY, CARBOXYLASE, CHLAMYDOMONAS-REINHARDTII, CI CELLS, INDUCTION, INORGANIC CARBON, PHOTOSYNTHESIS, TRANSPORT

2296

Sultemeyer, D., and K.A. Rinast. 1996. The CO₂ permeability of the plasma membrane of *Chlamydomonas reinhardtii*: Mass-spectrometric O-18-exchange measurements from (CO₂)-C-13-O-18 in suspensions of carbonic anhydrase-loaded plasma-membrane vesicles. *Planta* 200(3):358-368.

The unicellular green alga *Chlamydomonas reinhardtii* possesses a CO₂-concentrating mechanism. In order to measure the CO₂ permeability coefficients of the plasma membranes (PMs), carbonic anhydrase (CA)-loaded vesicles were isolated from *C. reinhardtii* grown either in air enriched with 50 mL CO₂ · L⁻¹ (high-C-i cells) or in ambient air (350 μL CO₂ · L⁻¹; low-C-i cells). Marker-enzyme measurements indicated less than 1% contamination with thylakoid and mitochondrial membranes, and that more than 90% of the PMs from high- and low-C-i cells were orientated right-side-out. The PMs appeared to be sealed as judged from the ability of vesicles to accumulate [C-14]acetate along a proton gradient for at least 10 min. Carbonic anhydrase-loaded PMs from high- and low-C-i cells of *C. reinhardtii* were used to measure the exchange of O-18 between doubly labelled CO₂((CO₂)-C-13-O-18) and H₂O in stirred suspensions by mass spectrometry. Analysis of the kinetics of the O-18 depletion from (CO₂)-C-13-O-18 in the external medium provides a powerful tool to study CO₂ diffusion across the PM to the active site of CA which catalyses O-18 exchange only inside the vesicles but not in the external medium (Silverman et al., 1976, *J Biol Chem* 251: 4428-4435). The activity of CA within loaded PM vesicles was sufficient to speed-up the O-18 loss to H₂O to 45360-128800 times the uncatalysed rate, depending on the efficiency of CA-loading and PM isolation. From the O-18-depletion kinetics performed at pH 7.3 and 7.8, CO₂ permeability coefficients of 0.76 and 1.49 · 10⁻³ cm · s⁻¹, respectively, were calculated for high- C-i cells. The corresponding values for low-C-i cells were 1.21 and 1.8 · 10⁻³ cm · s⁻¹. The implications of the similar and rather high CO₂ permeability coefficients (low CO₂ resistance) in high- and low-C-i cells for the CO₂-concentrating mechanism of *C. reinhardtii* are discussed.

KEYWORDS: CHLOROPLASTS, CI CELLS, CONCENTRATING MECHANISM, CYANOBACTERIA, DIOXIDE, HCO₃, IDENTIFICATION, INORGANIC CARBON, PHOTOSYNTHESIS, TRANSPORT

2297

Sulzman, E.W., K.A. Poiani, and T.G.F. Kittel. 1995. Modeling human-induced climatic-change - a summary for environmental managers. *Environmental Management* 19(2):197-224.

The rapid increase in atmospheric concentrations of greenhouse gases has caused concern because of their potential to alter the earth's radiation budget and disrupt current climate patterns. While there are many uncertainties associated with use of general circulation models (GCMs), GCMs are currently the best available technology to project changes in climate associated with elevated gas concentrations. Results indicate increases in global temperature and changes in global precipitation patterns are likely as a result of doubled CO₂. GCMs are not reliable for

use at the regional scale because local scale processes and geography are not taken into account. Comparison of results from five GCMs in three regions of the United States indicate high variability across regions and among models depending on season and climate variable. Statistical methods of scaling model output and nesting finer resolution models in global models are two techniques that may improve projections. Despite the many limitations in GCMs, they are useful tools to explore climate-earth system dynamics when used in conjunction with water resource and ecosystem models. A variety of water resource models showed significant alteration of regional hydrology when run with both GCM-generated and hypothetical climate scenarios, regardless of region or model complexity. Similarly, ecological models demonstrate the sensitivity of ecosystem production, nutrient dynamics, and distribution to changes in climate and CO₂ levels. We recommend the use of GCM-based scenarios in conjunction with water resource and ecosystem models to guide environmental management and policy in a "no-regrets" framework or as part of a precautionary approach to natural resource protection.

KEYWORDS: ATMOSPHERIC CO₂, CARBON-DIOXIDE CONCENTRATION, CHANGE IMPACTS, DELAWARE RIVER BASIN, ELEVATED CO₂, GENERAL-CIRCULATION MODEL, GREAT-LAKES, THORNTHWAITE MOISTURE INDEX, TROPICAL DEFORESTATION, WATER-BALANCE

2298

Sun, J.D., G.E. Edwards, and T.W. Okita. 1999. Feedback inhibition of photosynthesis in rice measured by O-2 dependent transients. *Photosynthesis Research* 59(2-3):187-200.

The kinetic properties of photosynthesis (both transient and steady-state) were monitored using three non-invasive techniques to evaluate limitations on triose-phosphate (triose- P) conversion to carbohydrate in rice. These included analyzing the O-2 sensitivity of CO₂ fixation and the assimilatory charge (AC) using gas exchange (estimate of the ribulose 1,5- bisphosphate pool) and measuring Photosystem II activity by chlorophyll fluorescence analysis under varying light, temperature and CO₂ partial pressures. Photosynthesis was inhibited transiently upon switching from 20 to 2 kPa O-2 (reversed O-2 sensitivity), the degree of which was correlated with a terminal, steady-state suppression of low O-2 enhancement of photosynthesis. Under current ambient levels of CO₂ and moderate to high light, the transient pattern was more obvious at 18 degrees C than at 26 degrees C while at 34 degrees C no transient response was observed. The transient inhibition at 18 degrees C ranged from 15% to 31% depending on the pre-measurement temperature. This pattern, symptomatic of feedback, was observed with increasing light and CO₂ partial pressures with the degree of feedback decreasing from moderate (18 degrees C) up to high temperature (34 degrees C). Under feedback conditions, the rate of assimilation is shifted from being photorespiration limited to being triose-P utilization limited. Transitory changes in CO₂ assimilation rates (A) under low O-2 indicative of feedback coincided with a transitory drop in assimilatory charge (AC) and inhibition of electron transport. In contrast to previous studies with many C-3 species, our studies indicate that rice shows susceptibility to feedback inhibition under moderate temperatures and current atmospheric levels of CO₂.

KEYWORDS: CARBON METABOLISM, CHILLING INJURY, CHLOROPHYLL FLUORESCENCE, CO₂ FIXATION, ELECTRON-TRANSPORT, LOW-TEMPERATURE, MATURE LEAVES, PHOTOSYSTEM, QUANTUM YIELD, VARIETAL DIFFERENCES

2299

Sung, F.J.M., and J.J. Chen. 1991. Gas-exchange rate and yield response of strawberry to carbon- dioxide enrichment. *Scientia Horticulturae* 48(3-4):241-251.

Short-term carbon dioxide (CO₂) enrichment (1000- μ l l⁻¹ for 10 days), starting 2 weeks after initial bloom, enhanced the leaf CO₂ exchange rate (CER) in rockwool-cultured strawberry (*Fragaria x ananassa*). CO₂ enrichment throughout the fruiting period stimulated canopy CER, decreased chlorophyll and leaf protein loss, and enhanced fruit set and consequent fruit production.

KEYWORDS: ATMOSPHERES, ELEVATED CO₂, GROWTH, PHOTOSYNTHESIS, PLANTS

2300

Suzuki, K. 1995. Phosphoglycolate phosphatase-deficient mutants of *Chlamydomonas reinhardtii* capable of growth under air. *Plant and Cell Physiology* 36(1):95-100.

Mutants deficient in phosphoglycolate phosphatase (PGPase) require elevated levels of CO₂ for growth in the light and cannot grow when photorespiration occurs. Revertants, namely, double mutants capable of growth under air without restoration of the missing PGPase activity, might be expected to have secondary mutations that reduce or eliminate photorespiration. Nineteen revertants were selected from a culture of a PGPase-deficient mutant of *Chlamydomonas reinhardtii* (pgp-1-18-7F) after a second mutagenesis that involved treatment with 5-fluorodeoxyuridine and ethyl methanesulfonate. There were significant differences in the photosynthetic affinity for CO₂ among revertant cells grown under 5% CO₂. Eight revertants had five times higher photosynthetic affinity for CO₂ than that of wild type 2137 cells grown under 5% CO₂, resembling air-adapted wild-type cells, whereas four revertants had less than half the affinity for CO₂ of the wild type. In all of the revertant cells with higher affinity grown in 5% CO₂, the rates of photosynthesis under levels of CO₂ below those in air were apparently higher than that of the wild type, whereas the rates under CO₂-saturating conditions were lower than that of wild type, indicating that the efficiency of photosynthesis under air was significantly improved in these revertants. In addition, some revertants had a photosynthetic capacity and a growth rate higher than those of the wild type, without any increased photosynthetic affinity for CO₂.

KEYWORDS: LIMITING CO₂, PHOTORESPIRATORY MUTANT

2301

Suzuki, T., K. Ohtaguchi, and K. Koide. 1991. Effects of gas-flow rate of CO₂-enriched air, high CO₂ concentration, and anaerobic atmosphere on the growth of blue- green-alga *Anacystis-nidulans*. *Journal of Chemical Engineering of Japan* 24(6):797-798.

2302

Svedang, M.U. 1992. Carbon-dioxide as a factor regulating the growth dynamics of *Juncus bulbosus*. *Aquatic Botany* 42(3):231-240.

The unusual growth pattern exhibited by *Juncus bulbosus* L. in a slightly acidic Swedish brown-water lake is due to a CO₂ deficit. Decrease in growth rate during the summer can be avoided through CO₂ addition in July when CO₂ availability is low and epiphytes are thriving. Growth of *J. bulbosus* in the laboratory is stimulated by CO₂ addition up to a concentration somewhat higher than in air (500 ppm), while higher CO₂ pressure restrains growth. Root growth reflects the leaf biomass development, but is favoured by elevated CO₂ levels even more than the leaves.

KEYWORDS: ACIDIFICATION, EUTROPHICATION, IMPACT, MACROPHYTE COMMUNITIES, PHOTOSYNTHESIS, PLANTS, SOFT WATERS

2303

Svensson, B.H., T.R. Christensen, E. Johansson, and M. Oquist. 1999. Interdecadal changes in CO₂ and CH₄ fluxes of a subarctic mire: Stordalen revisited after 20 years. *Oikos* 85(1):22-30.

The first subarctic wetland CO₂ and CH₄ flux measurements were made at Stordalen in the beginning of the 1970s in connection with the IBP study. A return to this area in 1994-95 offered a unique opportunity to study possible interdecadal changes in northern wetland CO₂ and CH₄ emissions. Measurements of CO₂ and CH₄ fluxes were carried out in similar habitats as those investigated in 1974. The mire distribution of wet minerotrophic areas relative to the elevated ombrotrophic areas had changed dramatically over the twenty years. There were no significant differences between the CH₄-flux in 1974, 1994, and 1995. However, the CO₂ fluxes were significantly higher in 1995 than in 1974. Since differences in climatic conditions gave no cause for such a change it suggests a possible increase in decomposition rate to be due to other factors. We suggest changes in vegetation composition, altered mineralization pathways and disintegration of permafrost as causes for the interdecadal increase in decomposition rates.

KEYWORDS: ALASKA, ARCTIC TUNDRA, CARBON DIOXIDE, CLIMATE CHANGE, METHANE EMISSIONS, PEAT, PEATLANDS, WETLANDS

2304

Swift, M.J., O. Andren, L. Brussaard, M. Briones, M.M. Couteaux, K. Ekschmitt, A. Kjoller, P. Loiseau, and P. Smith. 1998. Global change, soil biodiversity, and nitrogen cycling in terrestrial ecosystems: three case studies. *Global Change Biology* 4(7):729-743.

The relative contribution of different soil organism groups to nutrient cycling has been quantified for a number of ecosystems. Some functions, particularly within the N-cycle, are carried out by very specific organisms. Others, including those of decomposition and nutrient release from organic inputs are, however, mediated by a diverse group of bacteria, protozoa, fungi and invertebrate animals. Many authors have hypothesized that there is a high degree of equivalence and flexibility in function within this decomposer community and thence a substantial extent of redundancy in species richness and resilience in functional capacity. Three case studies are presented to examine the relationship between soil biodiversity and nitrogen cycling under global change in ecosystem types from three latitudes, i.e. tundra, temperate grassland and tropical rainforest. In all three ecosystems evidence exists for the potential impact of global change factors (temperature change, CO₂ enrichment, land-use-change) on the composition and diversity of the soil community as well as on various aspects of the nitrogen and other cycles. There is, however, very little unequivocal evidence of direct causal linkage between species richness and nutrient cycling efficiency. Most of the changes detected are shifts in the influence of major functional groups of the soil biota (e.g. between microflora and fauna in decomposition). There seem to be few data, however, from which to judge the significance of changes in diversity within functional groups. Nonetheless the soil biota are hypothesized to be a sensitive link between plant detritus and the availability of nutrients to plant uptake. Any factors affecting the quantity or quality of plant detritus is likely to change this link. Rigorous experimentation on the relationships between soil species richness and the regulation or resilience of nutrient cycles under global change thus remains a high priority.

KEYWORDS: ATMOSPHERIC CO₂, CARBON BALANCE, CO₂-ENRICHMENT, COMMUNITY STRUCTURE, ELEVATED CO₂, ENCHYTRAEIDAE OLIGOCHAETA, FERTILIZER APPLICATION, FOREST SOIL, MOWN GRASSLAND, TEMPERATE GRASS SWARD

2305

Sykes, M.T., I.C. Prentice, and W. Cramer. 1996. A bioclimatic model for the potential distributions of north European tree species under present and future climates. *Journal of Biogeography* 23(2):203-233.

A bioclimatic model based on physiological constraints to plant growth and regeneration is used here in an empirical way to describe the present natural distributions of northern Europe's major trees. Bioclimatic variables were computed from monthly means of temperature, precipitation and sunshine (%) interpolated to a 10' grid taking into account elevation. Minimum values of mean coldest-month temperature (T-c) and 'effective' growing degree days (GDD*) were fitted to species' range limits. GDD* is total annual growing degree days (GDD) minus GDD to budburst (GDD(o)). Each species was assigned to one of the chilling-response categories identified by Murray, Cannell & Smith (1989) to calculate GDD(o). Maximum T-c values were fitted to continental species' mild-winter limits and other deciduous species' warm-winter limits. Minimum values of relative growing-season moisture availability (α^*) were estimated from silvics. Growth indices were calculated based on potential net assimilation (a quadratic in daily temperature) and α^* . Growth can be rapid near a range limit, e.g. *Picea abies* (L.) Karsten in southern Sweden. Climate changes expected for CO₂ doubling were projected on to the grid. Simulated distribution changes reflected interspecific differences in response to changing seasonality. Chilling responses proved important, e.g. the predicted range limit of *Fagus sylvatica* L. contracts in the west while expanding northwards as winters warm more than summers. Transient responses to climate change can be modelled using the same information provided that fundamental and realized niche limitations are distinguished—a caveat that underlines the dearth of experimental information on the climatic requirements for growth, and especially regeneration, of many important trees.

KEYWORDS: AMERICA, BUDBURST, FORESTS, FROST DAMAGE, PICEA-SITCHENSIS, RESPONSES, VEGETATION

2306

Syvertsen, J., and J.H. Graham. 1997. Carbon budgets of two Citrus sp. in response to elevated CO₂ VA mycorrhizae and phosphorus status. *Plant Physiology* 114(3):111.

2307

Syvertsen, J.P., and J.H. Graham. 1999. Phosphorus supply and arbuscular mycorrhizas increase growth and net gas exchange responses of two Citrus spp. grown at elevated [CO₂]. *Plant and Soil* 208(2):209-219.

We hypothesized that greater photosynthate supply at elevated [CO₂] could compensate for increased below-ground C demands of arbuscular mycorrhizas. Therefore, we investigated plant growth, mineral nutrition, starch, and net gas exchange responses of two Citrus spp. to phosphorus (P) nutrition and mycorrhizas at elevated atmospheric [CO₂]. Half of the seedlings of sour orange (*C. aurantium* L.) and 'Ridge Pineapple' sweet orange (*C. sinensis* L. Osbeck) were inoculated with the arbuscular mycorrhizal (AM) fungus, *Glomus intraradices* Schenck and Smith and half were non-mycorrhizal (NM). Plants were grown at ambient or 2X ambient [CO₂] in unshaded greenhouses for 11 weeks and fertilized daily with nutrient solution either without added P or with 2 mM P in a low-P soil. High P supply reduced AM colonization whereas elevated [CO₂] counteracted the depressive effect of P on intraradical colonization and vesicle development. Seedlings grown at either elevated [CO₂], high P or with *G. intraradices* had greater growth, net assimilation of CO₂ (A(CO₂)) in leaves, leaf water-use efficiency, leaf dry wt/area, leaf starch and carbon/nitrogen (C/N) ratio. Root/whole plant dry wt ratio was decreased by elevated [CO₂], P, and AM

colonization. Mycorrhizal seedlings had higher leaf-P status but lower leaf N and K concentrations than nonmycorrhizal seedlings which was due to growth dilution effects. Starch in fibrous roots was increased by elevated [CO₂] but reduced by *G. intraradices*, especially at low-P supply. In fibrous roots, elevated [CO₂] had no effect on C/N, but AM colonization decreased C/N in both Citrus spp. grown at low-P supply. Overall, there were no species differences in growth or A(CO₂). Mycorrhizas did not increase plant growth at ambient [CO₂]. At elevated [CO₂], however, mycorrhizas stimulated growth at both P levels in sour orange, the more mycorrhiza-dependent species, but only at low-P in sweet orange, the less dependent species. At low-P and elevated [CO₂], colonization by the AM fungus increased A(CO₂) in both species but more so in sour orange than in sweet orange. Leaf P and root N concentrations were increased more and root starch level was decreased less by AM in sour orange than in sweet orange. Thus, the additional [CO₂] availability to mycorrhizal plants increased CO₂ assimilation, growth and nutrient uptake over that of NM plants especially in sour orange under P limitation.

KEYWORDS: ATMOSPHERIC CO₂, CARBON DIOXIDE, COLONIZATION, DEPENDENCY, ENRICHMENT, NITROGEN, PLANTAGO-LANCEOLATA, ROOT, SOUR ORANGE, TREES

2308

Szente, K., Z. Nagy, and Z. Tuba. 1998. Enhanced water use efficiency in dry loess grassland species grown at elevated air CO₂ concentration. *Photosynthetica* 35(4):637-640.

Net CO₂ assimilation rate (P-N), Stomatal conductance (g(s)), transpiration rate (E), and water use efficiency (WUE) in four perennial C-3 species (grasses: *Dactylis glomerata*, *Festuca rupicola*, dicots: *Filipendula vulgaris*, *Salvia nemorosa*) grown for 231 d in open-top chambers at ambient (CA, 350 $\mu\text{mol mol}^{-1}$) or elevated (CE, 700 $\mu\text{mol mol}^{-1}$) CO₂ concentrations were compared. When measured at CE, PN was significantly higher in CE plants of all four species than in the CA ones. The increase in P-N was less prominent in the two grasses than in the two dicots. The E was significantly higher in the CE-grass *F. rupicola* and CE-dicot *F. vulgaris* than in the CA plants. There was no change in E owing to CE in the other grass and dicot. The g(s) in *F. vulgaris* and *F. rupicola* increased, while there was a decrease in *D. glomerata* and no change in *S. nemorosa*. WUE increased in all species grown in CE: four- to five-fold in the dicots and less than two-fold in the grasses. The increase in WUE was primarily due to an increase in P-N and not to a decrease in E.

KEYWORDS: ATMOSPHERIC CO₂, CARBON DIOXIDE, GAS-EXCHANGE, LONG-TERM, PHOTOSYNTHESIS, PLANTS, RESPONSES, STEPPE, STOMATAL CONDUCTANCE, TRANSPIRATION

2309

Tajiri, T. 1997. Studies on the cultivation and storage quality of bean sprouts .13. Growth and quality of thick bean sprouts cultivated with a CO₂-enriched rotary method. *Journal of the Japanese Society for Food Science and Technology-Nippon Shokuhin Kagaku Kogaku Kaishi* 44(4):332-339.

Thick bean sprouts cultivated using a rotary box (rotary cultivation, RC) have a decreased yield and inferior quality, although the growth of sprouts from the beans is promoted and the nutrient content of the sprouts is improved(1)2)). Because exposure to high levels of carbon dioxide was useful for promoting the growth of the hypocotyl and increasing the quantity of harvested sprouts(3)), we combined the rotary box method with the CO₂-enriched method(1)). Herein the usefulness of this combination method for improving the physical properties and the yield of bean sprouts by controlling hypocotyl growth were